EVOLUTIONARY TRENDS IN SOME MESOZOIC TEREBRATELLACEA

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Pp. 205–253 ; 3 *Plates* ; 29 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 28 No. 3
LONDON: 1977

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Scientific Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 28, *No.* 3, *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.)

ISSN 0007-1471

BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 *March*, 1977 *Price* £5·10

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CONTENTS

SYNOPSIS

While the use of all morphological characters in the classification of the articulate brachiopods is desirable, it is suggested that more use could be made of the cardinalia in the border classification of some Cretaceous Terebratellacea. In this paper, some detailed features of the

cardinal process in certain genera are used to demonstrate trends which are thought to have an evolutionary significance.

A systematic study is made of some of the costate Terebratellacea from the Cretaceous, some of which have not previously been assigned to subfamilies. Two new genera (*Helvetella, Ruegenella*) and three new species (*Ruegenella ciplyensis, Oblongarcula alemannica, Arenaciarcula acuticostata*) are described. Lectotypes are selected for *Gemmarcula menardi* (Lamarck) from the Cenomanian of Le Mans, France, and for *Trigonosemus elegans* Koenig from the Maastrichtian of Normandy.

I. INTRODUCTION

IDEALLY, the broader classification of any group of brachiopods to the level of family and subfamily depends largely upon interpretation of the greatest number of characters. In the fossil articulates, such characters have included shell structure, punctation, early and mature loop development, size and type of cardinal process and other aspects of the cardinalia, as well as external morphology, folding, general outline and ornament.

Of these, perhaps the most important for the classification of the Terebratellacea has been the pattern of early stages in the development of the brachial loop. The work of Elliott (1947, 1950, 1953) now allows a better understanding of these patterns; his descriptions and illustrations of the ontogenetic development of loops of *Hamptonina*, from the Upper Jurassic, and *Gemmarcula*, from the Upper Aptian, have been one of the chief sources of reference in the classification of fossil Terebratellidae and Dallinidae for several years.

Baker (1972) demonstrated a similar ontogenetic series, using reconstructions from transverse serial sections and dissections of minute individuals of the zeilleriid *Zeilleria leckenbyi* from the Jurassic of the Cotswolds. His work confirmed, in many ways, the views of Babanova (1965) who found that, in certain species of *Aulacothyris* from the Jurassic of the Soviet Union, there was a connection between the loop and median septum in the early stages of ontogeny. Baker also demonstrated very convincingly that, during the early ontogenetic stages of *Z. leckenbyi*, both terebratellid and dallinid characteristics are visible.

The reliability of methods such as those employed by Elliott (1947, 1950) in the determination to family and subfamily level depends to a great extent upon the availability of suitable young forms which can be dissected. Within the Mesozoic, however, the difficulties in determining such early differences in loop development are well known. Baker (1972) overcame a great many of these in his approach to *Z. leckenbyi* by using a number of carefully selected young stages. Unfortunately such stages are not common among Mesozoic collections, in many cases the only specimens available for study being already mature.

An alternative approach to this problem, although by no means a replacement, can be made in some genera and species through a more critical and detailed study of the general morphological features and relative size of the cardinal process. Cooper (1970), in a review of generic characters in brachiopods, has stressed the importance of the cardinal process in defining genera, particularly in early Palaeozoic forms. He also pointed out (1970 : 230) that Mesozoic terebratulids and terebratellids had a similar development of cardinal process. The present study draws

upon Cooper's ideas that greater use of this structure, and a broader understanding of the cardinalia generally, may help in defining genera – or at least in increasing our knowledge of all the characters available for classification.

Within certain Palaeozoic suborders of brachiopoda, such as the Productidina and Chonetidina, the cardinal process has been used to advantage in broader family classification. Muir-Wood & Cooper (1960) recognized at least eight distinct morphological types within the Productidina alone, distinguishing the various types mainly on the general outline of the external face of the process, the presence or absence of a supporting median septum and the number of lobes constituting the boss.

The Mesozoic Terebratellacea examined here present less of a problem since fewer morphological varieties exist. Within the Cretaceous, three main morphological features of the cardinal process appear to predominate. One of these is the flattened, shallow, disc-like structure observed in *Oblongarcula* (Fig. 15, p. 230) which is certainly a poorly-developed structure not always clearly defined in transverse serial sections. It nevertheless appears to be more than just a mere flattening of the posterior end of the brachial valve and must surely have been functional.

Secondly, a more highly developed cardinal process of type similar to that just described is represented by the genus *Arenaciarcula* (Fig. 20, p. 237). Here the disc-like structure has been partially divided by indentations at approximately midway along its posterior and anterior walls, producing a bifid process.

A shallow disc-like structure is also observed in *Gemmarcula*, but in this genus the lateral rims of the process are more highly developed than in *Oblongarcula* or *Arenaciarcula* and can be recognized in transverse serial sections as two inwardly-curving plates which project a short distance into the umbonal cavity of the pedicle valve (Fig. 2, p. 212). This type of cardinal process can be seen to develop into a short, tube-like structure as seen in dissections of *G. canaliculata* (Fig. 6, p. 217) and *G. carantonensis* (Fig. 7, p. 218). The structure becomes grossly thickened in *G. carantonensis* but can still be recognized in serial sections as two distinct inwardly-curving plates (Fig. 8, p. 219).

The third main type of cardinal process observed within the Cretaceous is represented by *Dereta*, *Terebrirostra* and *Trigonosemus*. Although each of these can be clearly differentiated by generic characters which include some aspects of the cardinalia, in the main the massive cardinal boss supported by the high persistent septum and the elongate fused hinge-plates extending well into the pedicle umbonal cavity are conspicuous characters common to all three. In *Terebrirostra* and *Trigonosemus*, however, the cardinal process appears to develop three lobes which can be clearly seen in transverse serial sections (Fig. 23, p. 241 and Fig. 28, p. 247) whereas in *Dereta* (Fig. 29, p. 248) only two lobes can be recognized.

II. EXTERNAL MORPHOLOGY

Folding. The type of folding and sulcation of the anterior commissure seen throughout the range of genera and species of Terebratellidae examined falls within well-marked limits. These are *rectimarginate, uniplicate, intraplicate* and *antiplicate.*

No strong genetic link affecting the form of the anterior commissure is suggested, but it is felt there is some influence affecting the basic pattern of this character which is recognizable in succeeding genera within any given stock, albeit changed or modified by ecological conditions.

Cooper (1970 : 205) suggested that folding had seldom been used as a principal factor in generic definition. As a general rule this is so, but more importance is attached to it in the study of Terebratellacea described here. Similarity of folding may not prove of any consequence considered alone, but could be an additional guide in relating genera and species within a subfamily.

In the Upper Jurassic and Lower Cretaceous, intraplicate and antiplicate commissures occur within stocks of Terebratellacea which appear to have other characters in common. One of these is represented by *Ismenia pectunculoides* (Schlotheim) (Pl. 2, figs 3a–c) from the Upper Jurassic of Germany. The intraplicate commissure, transverse lamellar ornament and radial costae are strongly-developed characters which also occur in *Gemmarcula aurea* Elliott from the Upper Aptian and other related species within the Albian and Cenomanian. These features can also be recognized in *Ruegenella humboldti* (Hagenow) from the Maastrichtian of north Germany, which is believed to be directly related to *Gemmarcula* but to have evolved beyond the generic range of that form.

Costation. Shell ornament is very variable, not only from one species to another but also within the recognizable range of a given species. In general, the range includes ornament of strong, deeply-incised costae, such as those of *Arenaciarcula acuticostata*, to fine, frequently bifurcating, rounded costae as found in *Trigonosemus elegans*. In spite of a wide degree of variation most costae or costellae conform to a broad generic pattern. In the case of *Oblongarcula*, for example, costae tend to be fairly sharp or angular, varying mainly only in degree of coarseness.

Additional ornament of transverse lamellae occurs in some genera such as *Gemmarcula*, and is more marked on the surface of some species. It is possible that this character is largely affected by environmental change, as some individuals within a specific range show considerable degrees of variation from very faint to almost rugose.

Bifurcation of costae appears to be more common in some species than others and intercalation, which is a rare occurrence in the Cretaceous Terebratellacea, can also be seen in certain well-marked species.

External outline. Surlyk (1972), discussing the morphological adaptation of brachiopod faunas within the Danish Upper Chalk, grouped various genera and species according to their ecological habits. Some of the forms which he grouped as 'living free on the substrate' (Group II) were seen to assume the same or similar morphological characters. Of his 'hemispherical free living species', *'Gemmarcula' humboldti* and *Trigonosemus pulchellus* are discussed in the systematic section of this paper.

The degree of incurvature of the beak and the convexity of the valves are also important. This can be illustrated here, particularly within the Gemmarculinae,

which have a broad range of ecologically-controlled umbonal patterns ranging from massive, truncated by large foramen, to slightly-produced suberect, with small foramen. This reflects the environment of the fauna.

III. SYSTEMATIC DESCRIPTIONS

Family **DALLINIDAE** Beecher 1893

Subfamily **GEMMARCULINAE** Elliott 1947

Genus ***GEMMARCULA*** Elliott 1947

[= *Trifidarcula* Elliott 1959]

TYPE SPECIES. *Gemmarcula aurea* Elliott 1947.

DESCRIPTION. Since the original description of the genus by Elliott (1947), transverse serial sections have been made of the type species *G. aurea* from the Lower Greensand, Faringdon, Berkshire. These confirm the original diagnosis and description of the cardinalia and loop of the adult form and are presented here in Fig. 2.

REMARKS. A series of ontogenetic stages in the development of the brachial loop of *G. aurea* was demonstrated by Elliott (1947) which showed the pre-campagiform and campagiform stages to perfection. Barczyk (1969 : 12) showed a similar series of dalliniform stages in the development of *Ismenia pectunculoides* (Schlotheim) from the Upper Jurassic, Holy Cross Mountains, Poland. Externally the two genera have much in common with similar intraplicate folding of the commissure and general outline. The transverse shell ornament of evenly-spaced lamellae in addition to the radiating costae is also a feature of both forms. This is more apparent in *Gemmarcula trifida* (Meyer) (Pl. 1, figs 4a–c) and *G. pterygotos* (Walker) (Pl. 2, figs 1a–c, 2a–c).

It is possible that *Gemmarcula* has, in the general course of brachiopod evolution, been developed directly from *Ismenia*, but intermediate forms which may link them or, at any rate, bring them closer together, have not yet been investigated.

Gemmarcula aurea Elliott 1947

Figs 1, 2 ; Pl. 1, figs 3a–c.

1826 *Terebratula truncata* J. de C. Sowerby (*non* Linné) : 71 ; pl. 537, fig. 3.
1852 *Terebratula menardi* (Lamarck) ; Davidson : 24–26 ; pl. 3, figs 34–39, 41.
1874 *Terebratula truncata* (Sow.) ; Davidson : 25.
1947 *Gemmarcula aurea* Elliott : 146 ; pls 3, 4, figs 1–33.

EMENDED DESCRIPTION. The fourteen transverse serial sections given in Fig. 2 show the minor development of the cardinal process, the short divergent dental lamellae and the shallow hinge-trough buttressed by the stout, low median septum. They also show the rather poor development of the hinge-plates and the relative persistence of the supporting median septum.

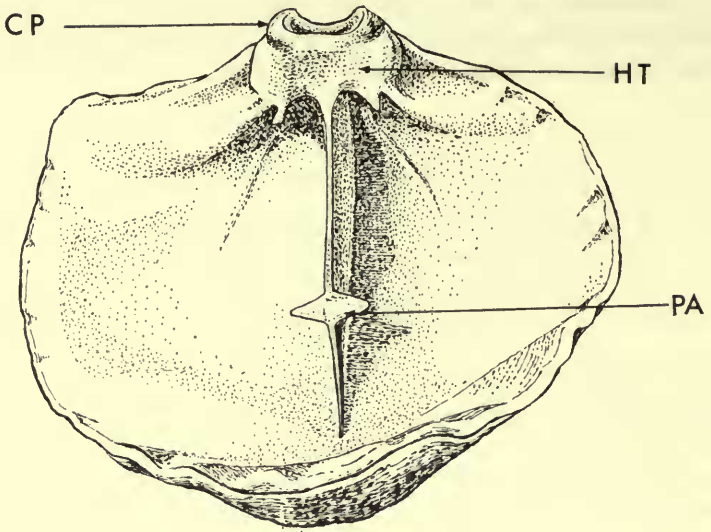

FIG. 1. Drawing of a dissected brachial valve of *Gemmarcula aurea* Elliott from the Upper Aptian, Faringdon, Berkshire. The simple cardinal process CP consists of a thickened disc-like depression at the posterior extremity of the broad, shallow hinge-trough HT. The point of attachment of descending branches of the brachial loop PA appears low on the high, persistent median septum. × 4.

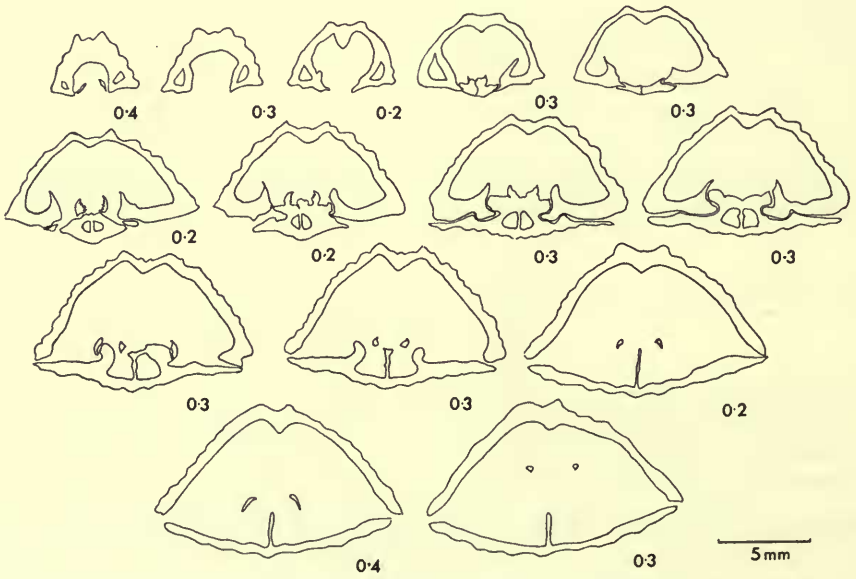

FIG. 2. A series of 14 transverse serial sections through the umbo of a specimen of *Gemmarcula aurea* Elliott, showing the comparatively short dental lamellae, simple bifid cardinal process, fused hinge-plates and high supporting median septum.

The point of attachment of descending branches to the septum has not been shown in serial sections here as this occurs beyond the mid-line of the brachial valve and is often damaged in individuals from the type locality. Nevertheless, this feature has been adequately described and figured by Elliott (1947).

The flaps or septal flanges described by Elliott (1947 : 150) occurring on the lateral extremities of the transverse band of the brachial loop in mature forms of *G. aurea* are not now considered to be of subfamily importance (Elliott 1957 : 336) ; they are probably caused by supplementary calcification from early developmental stages which became part of the loop when persisting to the adult stage. This view is confirmed by Richardson (1975 : 294), in a brief review of their general significance.

Atkins (1959 : 421) compared these structures to similar horn-like projections on the transverse band in early loop stages of the Recent *Terebratalia transversa* (G. B. Sowerby) but, unlike those of *Gemmarcula*, these structures are not maintained in the adult stages.

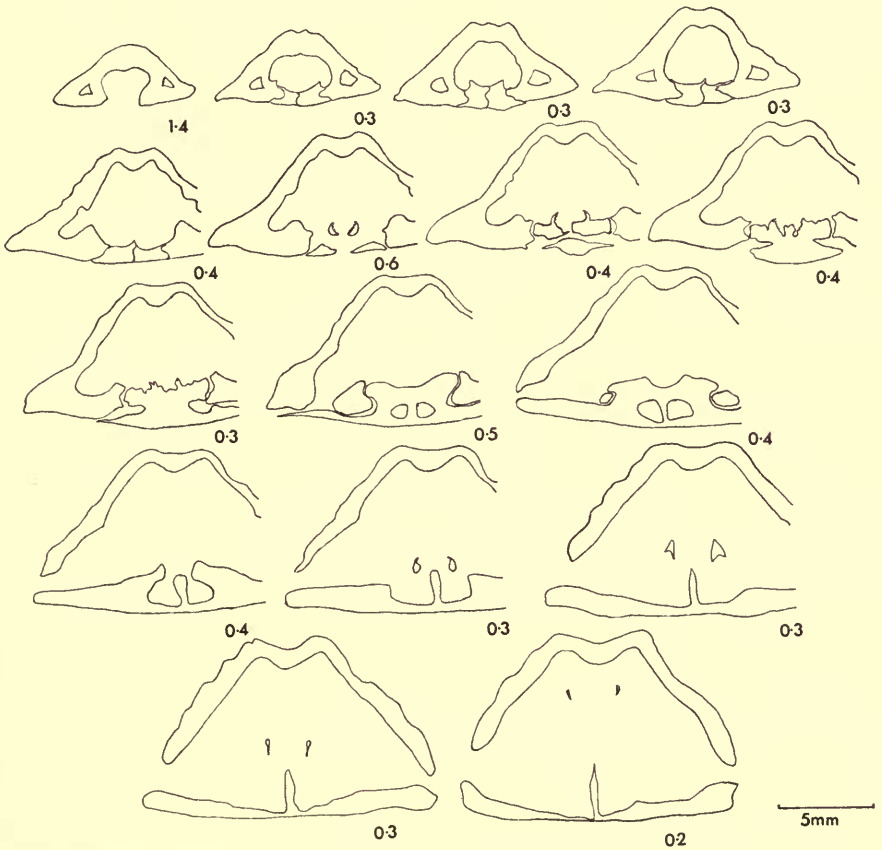

FIG. 3. Transverse serial sections through a specimen of *Gemmarcula pterygotos* (Walker) from the Lower Albian, Munday's Hill, Leighton Buzzard, Bedfordshire, showing the same generic features as the type species *G. aurea* Elliott.

Steinich (1965) used these structures as points of distinction when he assigned '*Terebratella*' *humboldti* Hagenow from the Rügen Chalk, Maastrichtian of north Germany, to the genus *Gemmarcula*. A more critical examination of the cardinalia of specimens of '*T.*' *humboldti* from the Rügen Chalk by both Finn Surlyk and myself has revealed that, although there is an undoubted relationship between '*T.*' *humboldti* and *Gemmarcula aurea*, it is not as close as Steinich suggested. A comparative study of certain fundamental differences in the cardinalia is discussed below in the description of *Ruegenella* gen. nov., to which '*T.*' *humboldti* has now been assigned.

Holotype. The specimen figured by Elliott (1947 : pl. 3, figs 8–10) is housed in the British Museum (Natural History) and registered as BB 9251.

Horizon and Locality. *Gemmarcula aurea* Elliott has not been recorded outside the Lower Greensand of Britain, where it appears to be confined to the Sponge Gravel of Faringdon. A species which approaches it in general morphology is *G. crassicosta* (Leymerie) from the Lower Cretaceous of Vimport, France. This was recently the subject of papers by Calzada (1975, 1976) with accompanying serial sections.

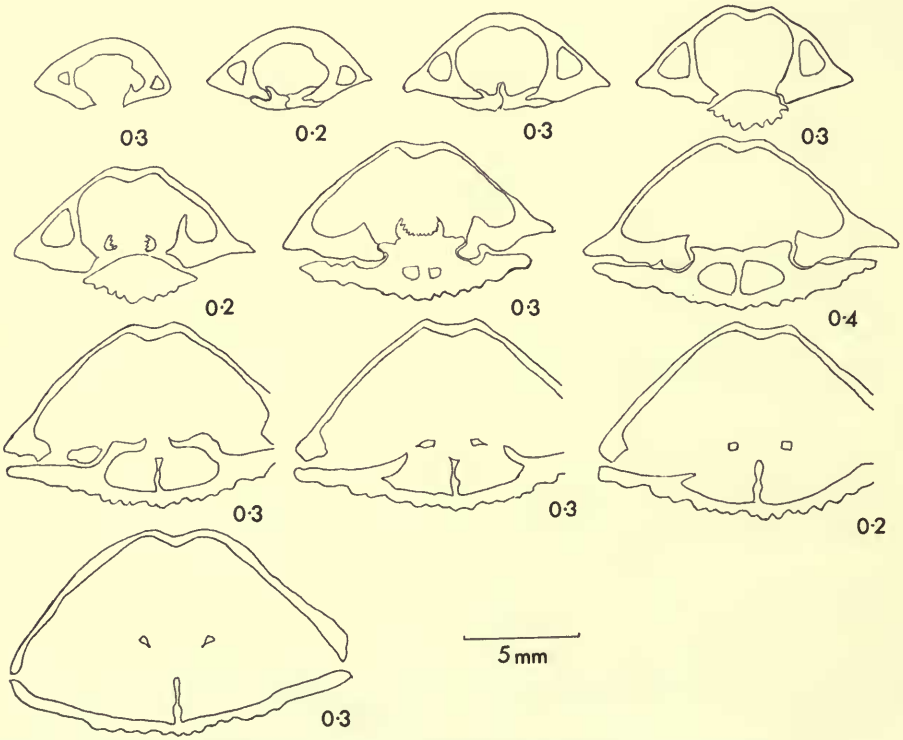

Fig. 4. Eleven serial sections through a specimen of *Gemmarcula asteriana* (d'Orbigny) from the Aptian of La Clape, France, confirming Elliott's original assignment of this species to *Gemmarcula*. (See also Pl. 1, Fig. 6 and Pl. 2, Fig. 9.)

Gemmarcula menardi (Lamarck 1819)

Fig. 5 ; Pl. 1, figs 2a–c.

1819 *Terebratula menardi* Lamarck : 256, no. 50.
1834 *Terebratula menardi* Lamarck ; von Buch : 78 ; pl. 3, fig. 42.
1838 *Terebratula menardi* Lamarck ; von Buch : 184 ; pl. 17, fig. 6.
1848 *Terebratella menardi* d'Orb. ; d'Orbigny : 118 ; pl. 517, figs 1–15.
1852 *Terebratella menardi* Lamarck ; Davidson : 24 ; pl. 3, fig. 42.
1867 *Terebratella menardi* Lamrk. ; Schloenbach (partim) : 458 ; pl. 22, fig. 1.
1871 *Terebratella menardii* Quenstedt : 261 ; pl. 517, figs 1–15.
1918 *Terebratula menardii* (Val. in Lam.) ; Favre : pl. 16, figs 93–99.
1947 *Gemmarcula menardi* (Lamarck) Elliott : 154.
1955 *Gemmarcula menardi* (Lamarck) ; Cooper : 10, pl. 2B, figs 29–34.

Emended description. In view of the accompanying transverse serial sections and other information obtained from comparative material, it is thought necessary to give a brief emendation to the descriptions so far available.

Elliott (1947 : 154) pointed out that the chief differences between the Cenomanian *G. menardi* and the type species *G. aurea* were that, in the Cenomanian form, the general width was proportionately greater and that the costae were clearer-cut or more acutely incised. It may be added that in *G. menardi* the median fold on the brachial valve is usually better developed or more marked, the interarea more extensive and the foramen considerably smaller than in the Aptian species *G. aurea*. Elliott also remarks that the cardinalia are similar, though the adult septum is longer in *G. aurea*. This observation is confirmed in the serial sections shown here, Fig. 5. In addition, the cardinalia are, if anything, slightly more advanced in development in the adult *G. menardi*, the posterior part of the hinge-trough occupied by an anteriorly thickened cardinal process. Fundamentally the arrangement of the cardinalia, the type of cardinal process and the shape of the hinge-trough are very much the same in both species.

Lectotype. Of the eleven syntypes in the Lamarck Collection, Muséum d'Histoire Naturelle, Geneva, the seven best-preserved (A–G) were figured in the catalogue of the Lamarck Collection by Favre (1918). The specimens are labelled as from 'Coulaines, près du Mans' and, from the preservation and matrix, are probably of Middle Cenomanian age from the well-known locality at Le Mans, Sarthe, France. The specimen selected here as lectotype of the species is the specimen labelled 'A' in the Lamarck Collection and figured by Favre (1918 : pl. 16, figs 93a–d).

Dimensions. Lectotype 9·5 mm long, 12·0 mm wide and 6·2 mm thick. Other specimens, all from the type locality and housed in the British Museum (Natural History), London, have dimensions as follows (measurements in mm).

	Length	Width	Thickness
B 5156	13·0	18·2	9·9
	15·0	16·0	9·0
	12·7	14·5	6·4

	Length	Width	Thickness
65685	15·9	14·0	10·0
	13·0	14·0	10·0
	12·5	15·4	8·9
	12·9	15·6	8·0
	14·0	13·1	8·5
	11·5	13·9	7·9

DISTRIBUTION. Apart from the type locality (at Le Mans, Sarthe, France) the species has been recorded from the Middle Cenomanian of Essen, north Germany,

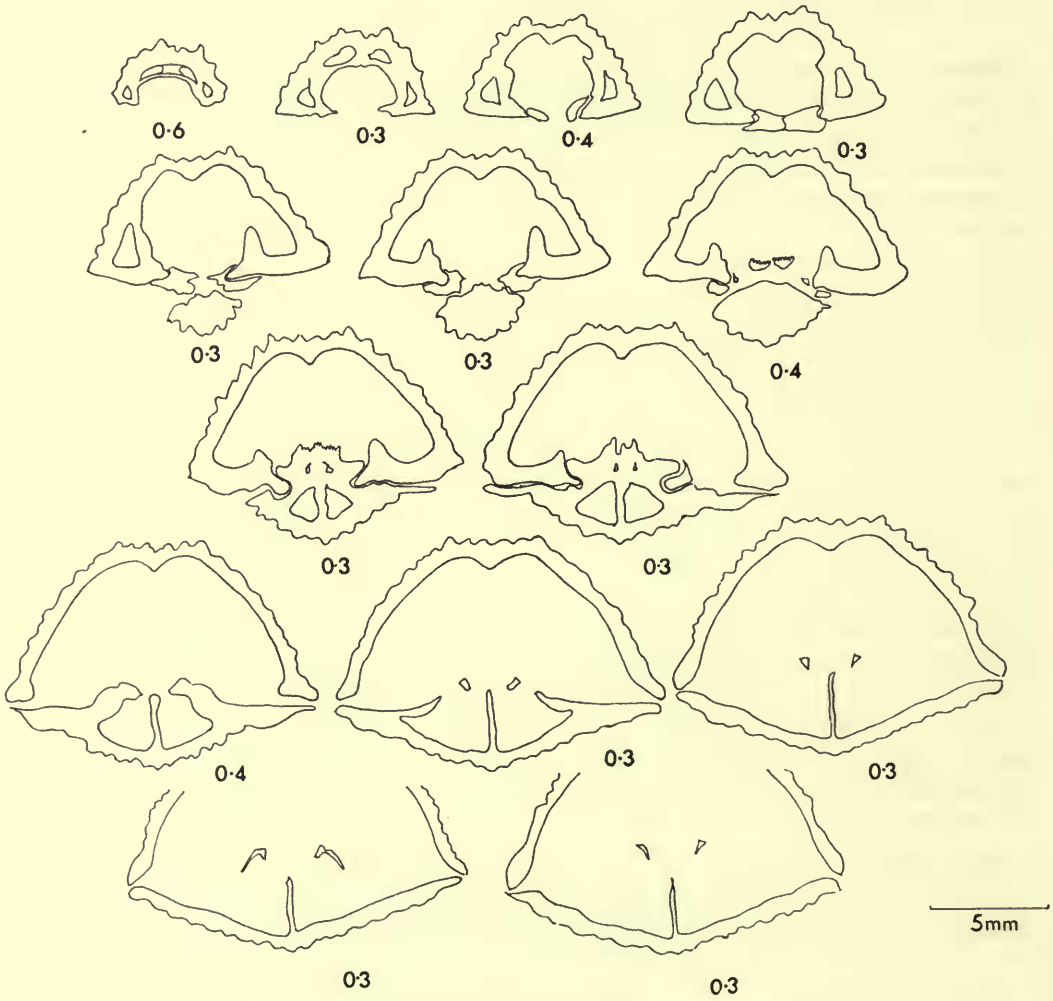

FIG. 5. Serial sections of *Gemmarcula menardi* (Lamarck) from the type locality of Le Mans, Sarthe, France. These show a slightly more highly developed cardinal process than is seen in the type species, and thickened cardinalia and lining-plates.

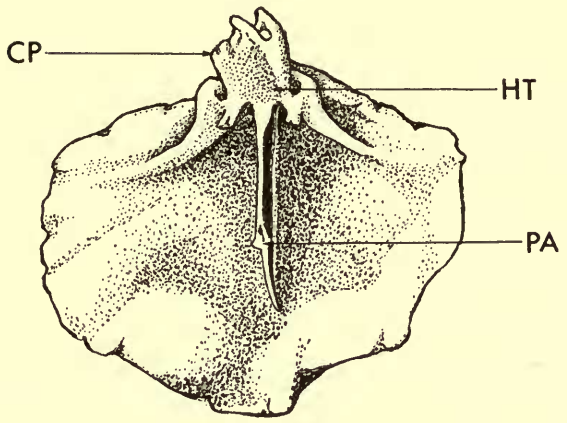

FIG. 6. Dissected brachial valve of a specimen of *Gemmarcula canaliculata* (Roemer) from the Tourtia of Tournai, Belgium, showing the extreme development of the cardinal process CP in this species. × 8.

the Tourtia of Tournai, Belgium and from the Middle Cenomanian of Dorset, Wiltshire and the Isle of Wight, England.

REMARKS. Among the ecological variants which have been assigned to this species are two forms described from the Cenomanian limestones of Poland. These are discussed in the remarks under *G. hercynica*.

The species described by d'Orbigny (1848 : 122) as *Terebratella carantonensis* is probably a further development or ecological variant of the type species. It occurs in the more chalky facies of the top beds of the Cenomanian in the Charente and Sarthe of northwestern France and bears most of the characters of the genus. It differs, however, in having a finer ornament of costae, less well marked median fold on the brachial valve and a less pronounced sulcus in the pedicle valve. The internal characters as seen in transverse serial sections, Fig. 8, show the same characteristic cardinalia and loop development as in the type species but also considerable secondary thickening, which makes these features difficult to recognize.

Gemmarcula menardi can be distinguished from *G. aurea* in having a wider hinge-line, more marked brachial fold and pedicle sulcus and sharper and more deeply incised radiating costae. It differs from *G. trifida* (Pl. 1, figs 4a–c) in having a less acutely developed median fold in the brachial valve and a greater number of clearly-defined radiating costae and shorter, or less extensive, interarea.

Gemmarcula carantonensis (d'Orbigny 1847)

Figs 7, 8 ; Pl. 1, figs 1a–c.

1848 *Terebratella carantonensis* d'Orbigny : 122 ; pl. 518, figs 1–4.

EMENDED DESCRIPTION. Large subquadrate *Gemmarcula*, almost equally broad as long. Shell with faint brachial fold and fairly well-marked pedicle sulcus originating from the umbonal regions. Anterior commissure antiplicate, similar to

that of *G. menardi*. An ornament of 36–40 rounded radiating costae, with frequent marginal bifurcation, adorns both valves, six or seven costae occurring on the fold with a corresponding number in the sulcus. The umbo is massive with distinct beak-ridges bordering an extensive interarea. A comparatively small, circular, submesothyridid foramen dominates a slightly incurved beak.

Distribution. d'Orbigny (1848) described the species from a level, now the *A. mantelli* Zone, of the Cenomanian from Port des Barques in the Charente. It was also stated to have been found at Eoux (Basses-Alpes). More recent records, particularly those of Kennedy & Juignet (1973), extend the geographical range to Cenomanian localities within Sarthe.

Remarks. It is with certain misgivings that this species is assigned to the genus *Gemmarcula*, since the internal structures as seen in both dissections and transverse serial sections depart slightly from the typical *Gemmarcula aurea* and *G. menardi*. After a great deal of consideration these comparatively minor differences, which amount to a more advanced cardinal process and considerable thickening of cardinalia, hinge-plates and septum, are now thought to be of secondary development. Nevertheless, the species does show some advancement towards another stage in the evolutionary range of the genus. It is therefore regarded as the ultimate representative species within this range.

d'Orbigny's original description was accompanied by an illustration (pl. 518, figs 1–4) which shows a specimen subcircular in outline with a suberect beak, extensive interarea and numerous strong costae with occasional bifurcation. I have examined over twenty specimens from the Charante and Sarthe but all have a

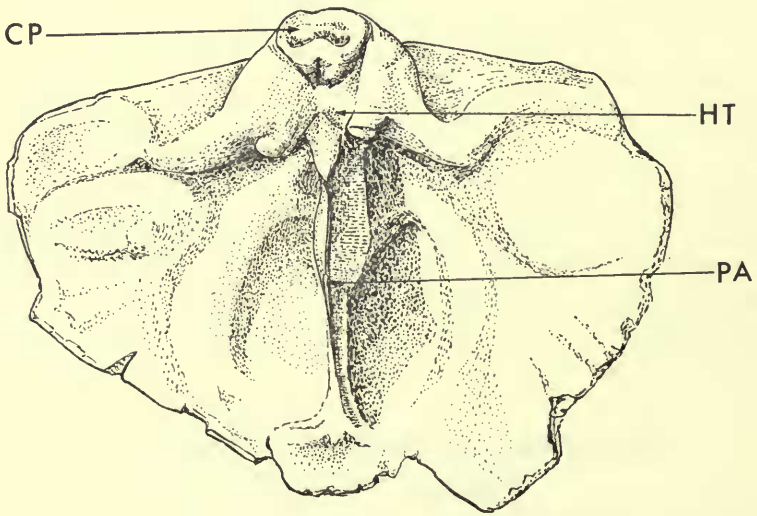

Fig. 7. The same generic characters are visible in this dissection of *Gemmarcula carantonensis* (d'Orbigny) from the Port des Barques, Charente, France, as appear in the type species, but are grossly thickened and difficult to differentiate. The hinge-trough HT, which is shallow, is not so clearly defined as in *G. aurea*. × 3.

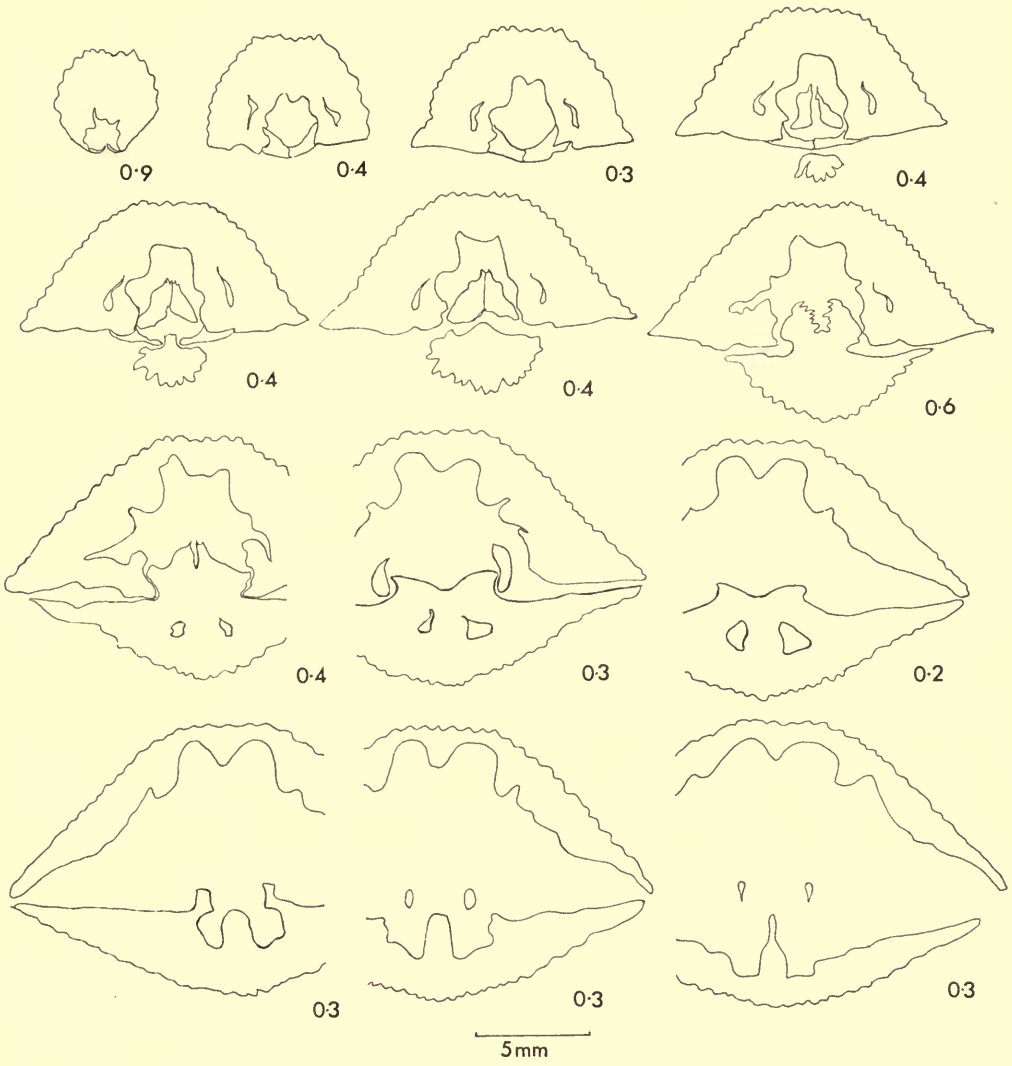

FIG. 8. Transverse serial sections of *Gemmarcula carantonensis* (d'Orb.), showing the secondary thickening of the vales and cardinalia, but the general characters can still be recognized.

more extended hinge-line than the one shown in d'Orbigny's figure. The beak characters are very much more variable than stated in the original description and the costae tend to be substantially finer, although this is a somewhat more variable character.

The species has been regarded as a reliable horizon marker within the Chalk, although at what particular horizon was not at all clear. Arnaud (1877 : 9–10), in his classic description of the Chalk of northwest France, suggests that *Terebratella*

carantonensis characterizes a zone within the Turonian and quotes it in association with *Ostrea carinata*, *Hemiaster leymerei* and *H. verneuili*, etc.

Kennedy & Juignet recently reviewed the existing correlation of the Cenomanian/Turonian boundary in northern France and England. Their conclusions are tabulated (1973 : 196) in a revised correlation equating the Craie à *Terebratella carantonensis* with the lower part of the Melbourne Rock in southeast England and part of the fauna of the *Neocardioceras* Pebble Bed at the base of the Middle Chalk in Devon. From their analysis it seems that *G. carantonensis* occurs in the Upper Cenomanian.

Dimensions. All material in the British Museum (Natural History), London. Figured specimen, BB 45960, 19·8 mm long, 20·0 mm wide and 10·5 mm thick. Other specimens have dimensions as follows (measurements in mm).

	Length	Width	Thickness
(a), from the Craie Chloritée, Charente, France			
B 6669	25·6	25·1	15·7
	21·5	21·1	11·4
	19·0	19·1	9·8
(b), from the Craie à *Terebratella carantonensis*, Port des Barques, Charente, France			
BB 45982	23·7	23·6	12·9
BB 45983	20·9	24·0	11·0
BB 45984	18·9	18·1	8·4
BB 45985	17·0	17·0	8·9
BB 45986	18·5	18·1	9·0

Gemmarcula hercynica (Schloenbach 1867)

1867 *Megerleia* (?) *hercynica* Schloenbach : 467 ; pl. 22, figs 6, 7.
1869 *Terebratella kurskensis* Hofman : 24 ; pl. 5, figs 12–15.

Description. Schloenbach's original description (1867 : 467) is adequate for the species, which is here referred to the genus *Gemmarcula* largely on account of external morphological similarities. The chief differences between *G. hercynica* and *G. menardi* appear to be confined to the hinge-line and costation. In *G. hercynica* the hinge-line is narrow and the interarea remains as a small triangle just anterior to the pedicle umbo. There appear to be two to three main costae radiating from either side of the main brachial fold, with faint costellae between each of the main costae.

Remarks. Since the original description of this species under the name of *Megerleia* (?) *hercynica*, few references have been made to this form. The whereabouts of the two specimens figured by Schloenbach (1867 : pl. 22, figs 6, 7) is unknown and the question of proposing a neotype may have to be considered in due course.

Nevertheless, the species is well founded and easily distinguishable. Subsequent British and continental authors have described species referable to *Gemmarcula*

which have a similar morphology to *G. hercynica* ; some of these are discussed here. One of them includes a specimen described and figured by Hofman (1869 : 24 ; pl. 5, figs 12–17) as *Terebratella kurskensis* from the Cenomanian of Russia which is here considered to be a synonym of *G. hercynica*. The narrow hinge-line costation and marked median brachial fold with flanking costellae suggest a very close relationship.

Confusion with Schloenbach's *G. hercynica* has arisen over a terebratelloid described by Walker (1903 : pl. 18, fig. 3) as *Terebratula menardi* var. *pterygotos* (Fig. 3, p. 213 ; Pl. 2, figs 1a–c, 2a–c). It is from the Lower Albian limestone of Shenley Hill, Leighton Buzzard, Bedfordshire, and is here referred to *Gemmarcula*. Though somewhat similar in general outline and morphology, it differs from *G. hercynica* (Schloenbach) in having a much more extensive hinge-line and interarea. It is generally broader and has more consistently even costation, but there appears to be a considerable range of variation within the species.

A species approaching *G. hercynica* in external morphology was described and figured by Ravn (1925 : 24 ; pl. 1, figs 1a–d) as *Terebratella kofoedi* (Pl. 2, figs 4a–c) from the Cenomanian basal conglomerates of Bornholm, Denmark. It is somewhat narrower than either of the two specimens figured by Schloenbach and has three distinct ribs on either side of the central brachial fold. Although the internal structures of this form are unknown, it is considered referable to the genus *Gemmarcula*.

The specimen from the Cenomanian of Saratovsk, Russia, figured by Sintsov (1872 : pl. 13, figs 16, 17) as *Terebratella menardi* is not typical of the species and in many ways resembles Schloenbach's *T. hercynica*. It has more radial costae and slightly more prominent growth-lines, but in general outline the two forms are very much alike.

Sintsov's specimen also resembles the specimen figured by Panow (1969 : 589, pl. 112, fig. 4) from the Cracow district of Poland, although the latter appears to have been an internal mould and does not show the radiating costae to advantage. In general outline Panow's specimen resembles one figured by Popiel-Barczyk (1972 : pl. 1, fig. 6) from the Cenomanian of Annapol, Russia, except that it is broader and has a more acute fold on the brachial valve. None of the forms mentioned above is typical of the species described as *Terebratella hercynica* by Schloenbach and it is possible that they represent distinct subspecies of either *G. menardi* or *G. hercynica*.

Genus ***HELVETELLA*** nov.

Type species. *Terebratula* (*Terebratella*) *arzierensis* de Loriol 1864.

Diagnosis. Pentagonal, uniplicate to parasulcate, evenly biconvex, costate Terebratellidae. Maximum width just posterior to mid-line. Umbo massive, beak suberect. Foramen large, circular, mesothyridid. Interarea extensive, slightly concave ; beak ridges distinct. Hinge-plates short, triangular, ventrally deflected. Symphytium short, broad. Cardinal process absent.

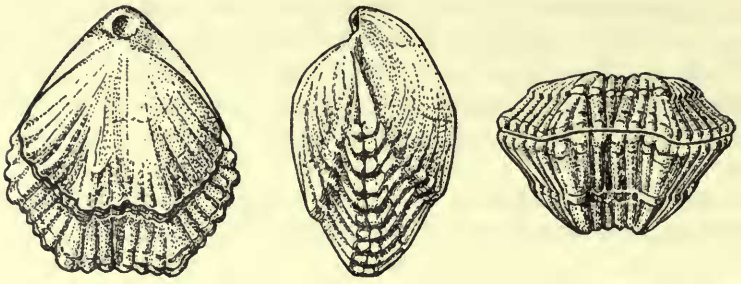

FIG. 9. *Helvetella arzierensis* (de Loriol), from the Valanginian of Arzier, Switzerland, showing the typical pentagonal outline, arrangement of costae and step-like growth lines. × 2.

Helvetella arzierensis (de Loriol 1864)

Figs 9, 10; Pl. 2, figs 5a–c.

1864 *Terebratula* (*Terebratella*) *arzierensis* de Loriol : 441 ; pl. 1, figs 11–13.
1866 *Terebratula* (*Terebratella*) *arzierensis* de Loriol ; Schloenbach : 372.
1868 *Terebratula* (*Terebratella*) *arzierensis* de Loriol ; de Loriol : 55 ; pl. 5, figs 2–5.
1872 *Terebratula* (*Terebratella*) *arzierensis* de Loriol ; Pictet : 123 ; pl. 207, figs 3–6.

EMENDED DESCRIPTION. Although broadly pentagonal in general outline, the species is variable in form, ranging in length from 14 to 19·5 mm and in width from 11 to 18·5 mm. It has a generally somewhat terebratuloid aspect, but with numerous strong, bifurcating, rounded costae. The dichotomy of the costae is more evident nearer the margins. A fine, lamellar transverse ornament is noticeable, as well as one to three stronger concentric growth-lines which appear at about midway and just anterior of the mid-line in mature specimens.

A shallow sulcus originating from the pedicle umbo continues anteriorly, broadening at the margins. A similar, but shallower, sulcus is sometimes seen on the median fold of the brachial valve, but this is not regarded as a marked specific character. The sulci are often bounded by faint carinae in both valves.

Internal structure. As seen in successive serial sections, the short convergent dental lamellae soon diminish. No cardinal process is developed but a faint, cup-like, shallow hinge-trough, buttressed by a high, strong median septum, is deflected ventrally, giving rise to two triangular hinge-plates. The supporting median septum diminishes rapidly leaving extensive curved inner socket-ridges. These become more rectangular in outline, developing into the crural bases which in turn thin out to become well-developed crural processes. Finally, the descending branches of the brachial loop develop anteriorly, assuming what is thought to be a terebrataliform loop.

MATERIAL AND DIMENSIONS. It is not known for certain whether the specimen figured by de Loriol (1864 : pl. 1, figs 11–13) is still extant. The question of selecting a lectotype from the two syntypes figured by de Loriol must, therefore, remain until exhaustive enquiries have been made. The specimen figured here, Pl. 2, figs 5a–c, is a topotype specimen in the Davidson Collection in the British

Museum (Natural History), BB 61527. The Davidson and general collections also contain eleven more topotypes, the dimensions of which are given below (measurements in mm).

	Length	Width	Thickness
BB 61527	18·0	16·0	11·0
B 6185	18·5	16·0	9·9
	19·9	18·1	10·1
	17·1	17·0	9·1
	15·2	13·2	8·8
	14·0	14·9	7·1
	13·1	13·7	6·2
	14·7	12·8	8·5
	12·1	10·8	6·1
B 35678	20·0	17·2	12·5
	14·0	14·9	7·4
	13·4	13·8	6·7

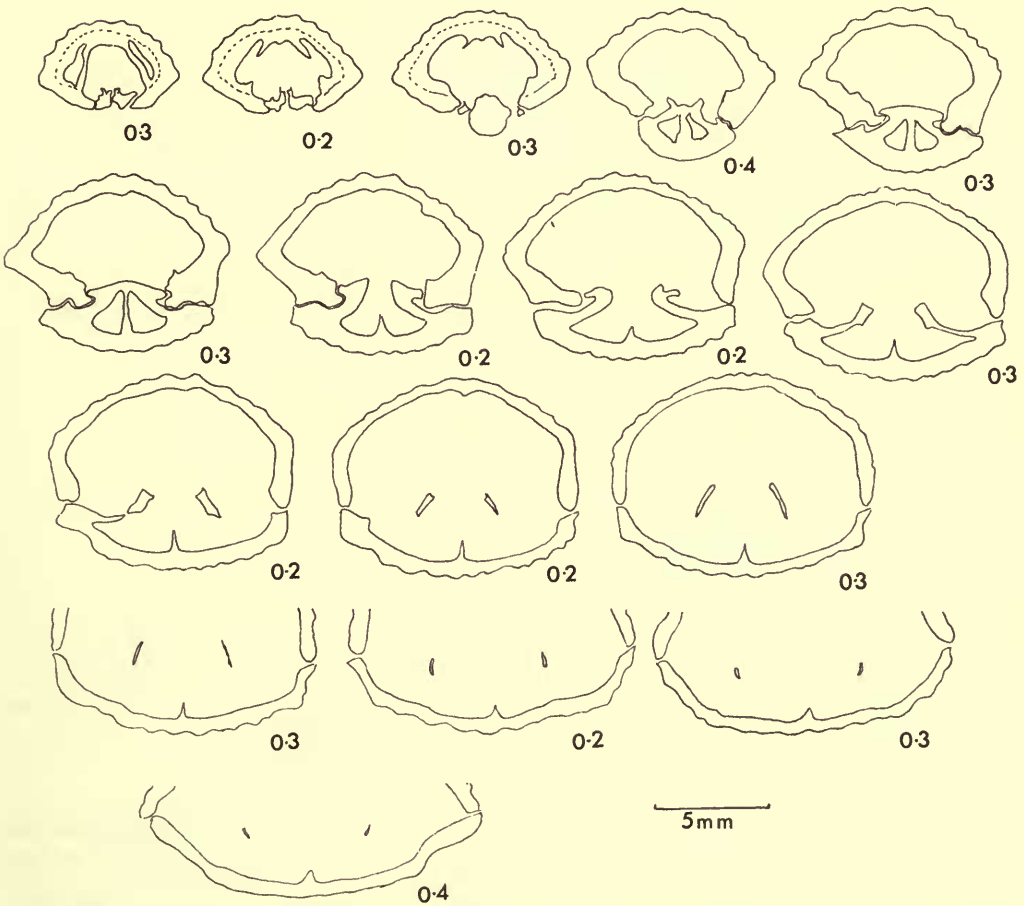

FIG. 10. Serial sections through a specimen of *Helvetella arzierensis* (de Loriol). The short dental lamellae are seen in the pedicle umbo and no cardinal process is developed.

Distribution. The type species, *Helvetella arzierensis* (de Loriol), is known only from the area of its original description, Arzier, Vaud, Switzerland, where it occurs in the Upper Valanginian of the Lower Cretaceous. Two other species are here referred to *Helvetella*, *Terebratella marini* and *T. riosi*, both described from the Valanginian of Valencia, Spain, by Bataller (1947).

Remarks. In general outline, folding and sulcation of the valves, *Helvetella arzierensis* has much in common with *Gemmarcula asteriana* (d'Orbigny) (Fig. 4; Pl. 1, figs 6a–c ; Pl. 2, figs 9a–c), which was originally described from the Aptian of Wassy and St Dizier (Haute-Marne), France. It differs in having coarser, more rounded costae, more step-like concentric growth-lines and different internal structure. Unlike *Gemmarcula*, *Helvetella* does not develop a cardinal process and the hinge-plates in the type species are developed directly from a ventrally deflected and shallow hinge-trough.

Genus ***RUEGENELLA*** nov.

Type species. *Terebratula humboldti* Hagenow 1842.

Diagnosis. Shell subquadrate to oval, costate. Brachial fold distinct. Well-defined pedicle sulcus bounded by faint carinae. Umbo slightly produced, beak suberect. Foramen small, circular, mesothyridid. Interarea extensive. Symphytium well exposed. Cardial process massive, bilobed. Hinge-plates thickened, fused. Median septum low. Anterior commissure intraplicate.

Ruegenella humboldti (Hagenow 1842)

Figs 11–13.

1842 *Terebratula Humboldti* Hagenow : 539 ; pl. 9, fig. 5a–c.
1850 *Terebratula Humboldti* Hagenow ; Geinitz : 210.
1856 *Terebratula Humboldti* Hagenow ; Boll : 210.
1871 *Terebratula Menardii* Quenstedt : pl. 44, fig. 69.
1909 *Terebratella Humboldti* Hagenow ; Nielsen : 168 ; pl. 2, figs 102–105.
1965 *Gemmarcula humboldtii* (Hagenow) Steinich : 160 ; pl. 19, fig. 1.
1972 *Gemmarcula humboldtii* (Hagenow) ; Surlyk : 24.

Description. *Ruegenella* with 35–40 strong rounded costae interrupted by transverse ornament of numerous fine lamellae and six or seven concentric growth-lines. The well-defined pedicle sulcus originates from the extreme posterior end of the umbo and widens anteriorly, remaining at a consistent depth ; it is bordered by faint carinae.

Internal characters. The transverse serial sections given here, Fig. 13, show the thickened shell, fused dental lamellae and very much reduced and thickened median septum supporting fused, poorly-defined hinge-plates. The disc-like cardinal process shows a more advanced development than that seen in *Gemmarcula*, having more acute indentations in the central part of the wall of the disc, making two almost complete tube-like extensions which are produced posteriorly (Fig. 12).

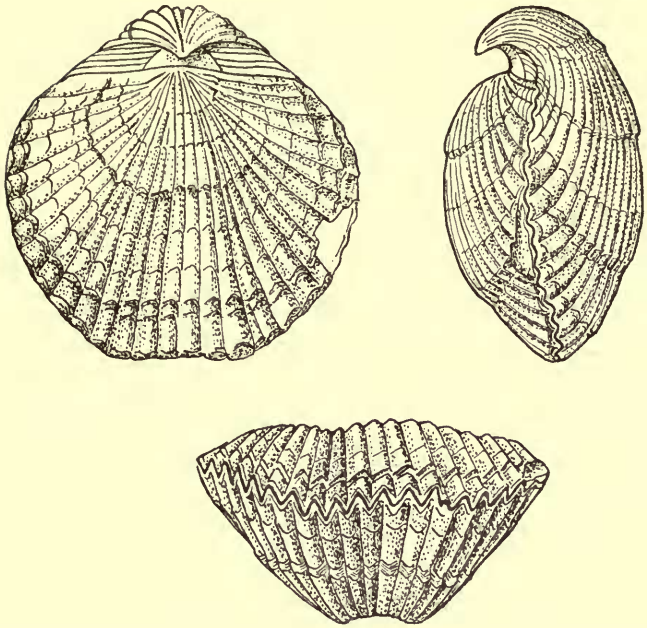

FIG. 11. *Ruegenella humboldti* (Hagenow) from the Maastrichtian of Rügen, north Germany. The general outline, costation and anterior folding are very similar to those of *Gemmarcula*. × 3.

The hinge-trough is shallow and not raised above the floor of the brachial valve. The descending branches of the brachial loop are given off directly from the distal ends of the hinge-trough without the development of any discernible crural bases as noted in *Gemmarcula*.

REMARKS. In placing *T. humboldti* Hagenow in the genus *Gemmarcula*, Steinich (1965) was influenced very greatly by the similarity between the early ontogenetic stages which he had dissected from Chalk specimens and those of *Gemmarcula aurea*, the type species, which had been so carefully prepared and described by Elliott (1947). Steinich referred particularly to the lateral flanges on the transverse band of the mature loop and used this as a strong argument for assigning the species to *Gemmarcula*. This, with the surprisingly similar external morphological details, was sufficient evidence at that time. However, Elliott (1957 : 334–336) states that the flanges described on the transverse band of the type species are not now considered to be of diagnostic importance, as has already been pointed out with reference to *Gemmarcula* (p. 213).

Two other species are recognized as referable to *Ruegenella*. One is the large Maastrichtian species described as *Terebratella corneti* by Hanstein (1879) from Ciply, Belgium, represented here by a specimen from the Craie Phosphatée of Ciply (Pl. 1, figs 9a–c). It can be distinguished from *R. humboldti* by its considerably larger dimensions, massive truncated umbo, broad or extensive interarea and wider hinge-line.

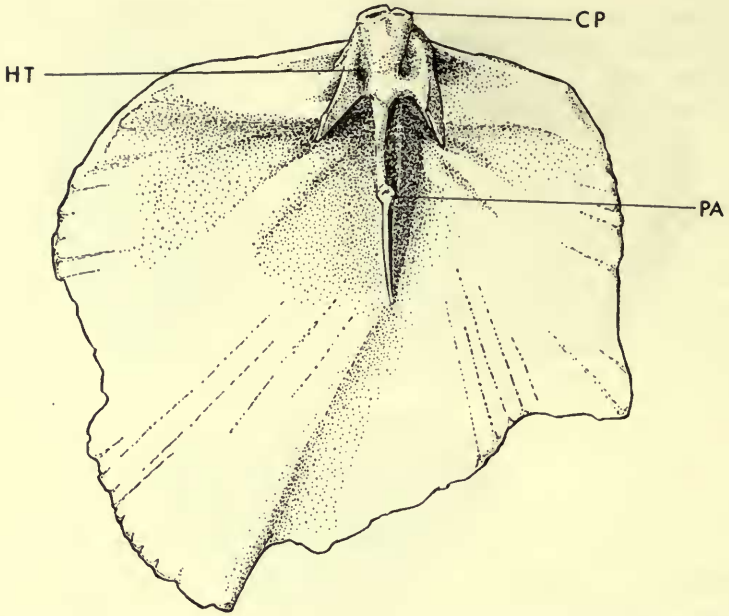

FIG. 12. Brachial valve of *Ruegenella humboldti* (Hagenow), showing the somewhat produced cardinal process CP with central depressions almost dividing it into two tubes. The hinge-trough HT is shorter and shallower than in *Gemmarcula* and the point of attachment for the brachial loop PA is placed more posteriorly on a proportionately shorter median septum. ×6.

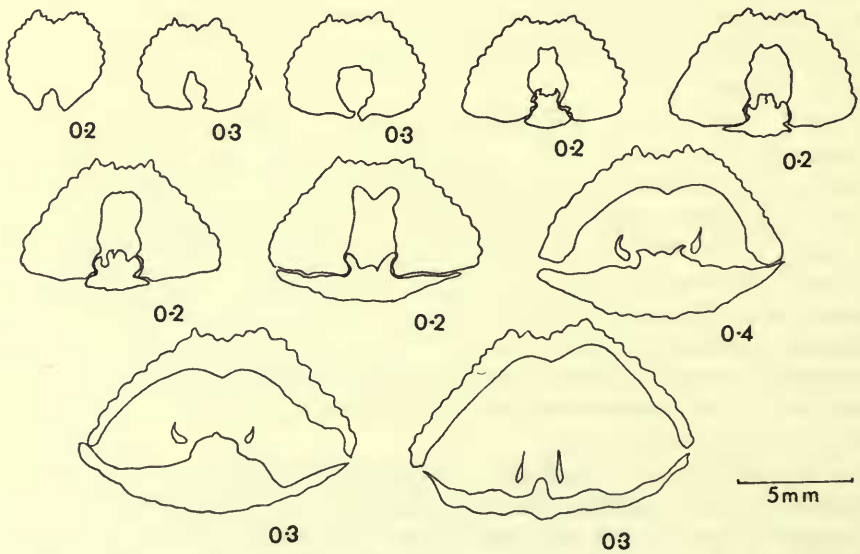

FIG. 13. Serial sections of *Ruegenella humboldti* (Hagenow), showing the grossly thickened pedicle umbo and fused dental lamellae, bifid cardinal process and massive, low median septum.

The other species, from the same locality and horizon, is described here briefly as *Ruegenella ciplyensis* sp. nov.

Ruegenella ciplyensis sp. nov.

Pl. 1, figs 5a–c.

Description. Small, subcircular *Ruegenella*, approximately 9 mm long, 10 mm wide and 6 mm in thickness. The umbo is massive and truncated by a comparatively large circular mesothyridid foramen. The shell ornament consists of 20–24 coarse radiating costae with well-marked transverse lamellar ornament on each valve. The interarea is flat and extensive and the break-ridges sharply defined. A broad low brachial fold develops anteriorly and there is a corresponding shallow sulcus in the pedicle valve. A fairly strong antiplicate anterior commissure is developed in the mature form.

Holotype. From the Craie Phosphatée of the Upper Chalk, Ciply, Belgium, in the Walker Collection, British Museum (Natural History), BB 45963. Dimensions: length 9·1 mm, width 9·9 mm, thickness 6·0 mm.

Paratypes. B 6655, B 15388, BB 45980–91. Also from the Craie Phosphatée, Ciply, Belgium, in the British Museum (Natural History).

Remarks. In general morphology this species resembles the associated *Ruegenella corneti* (Hanstein), but differs in being considerably smaller, and in the coarser radial ornament and more marked transverse lamellar ornament of the shell. The anterior commissure has a much more acute antiplication than *R. corneti* and in many ways resembles that of *Gemmarcula aurea* Elliott. *Ruegenella ciplyensis* differs from *R. humboldti* (Hagenow) in having a more massive umbo, coarser costae and wider hinge-line.

The species appears to be confined to the Craie Phosphatée of the Ciply district in much the same way as *R. corneti*.

Subfamily **UNCERTAIN**

Genus ***OBLONGARCULA*** Elliott 1959

Oblongarcula alemannica sp. nov.

Fig. 14; Pl. 3, figs 5a–c.

1836 *Terebratula oblonga* Sow.; Roemer: 46; pl. 2, fig. 23a–c.
1836 '*Terebratula reticulata* Schloth., var. *angusta* Sow.'; Pusch: 24; pl. 3, fig. 11a, b, c, d.
1839 *Terebratula pectiniformis* Roemer: 20; pl. 18, fig. 9 (non Schlotheim).
1840 *Terebratula puscheana* Roemer: 114; pl. 16, fig. 29.
1848 *Terebratella oblonga* d'Orbigny: 113; pl. 515, figs 7–19.
1850 *Terebratula oblonga* Sow.; Strombeck & von Buch: 76; pl. 4, figs 1–19.
1871 *Terebratula puscheana* Roemer; Quenstedt: 275; pl. 44, fig. 139.

Diagnosis. *Oblongarcula*, biconvex, elongate-oval to subpentagonal, costate to costellate. Umbo massive, beak suberect; beak-ridges distinct, mesothyridid. Anterior commissure rectimarginate through uniplicate to antiplicate. Disc-like

cardinal process poorly developed. Fused hinge-plates supported by high, persistent median septum.

Description. Although typically oval in general outline with strong, deeply incised radiating costae, the species shows a considerable range of variation. The hinge-line in some variants extends laterally, increasing the flat interarea and exposing well-defined conjunct deltidial plates. This type of development is not a common variation but, when it occurs, produces a much flatter variety with young forms proportionately wider than long. Roemer (1839 : 20 ; pl. 18, fig. 9) described what he thought was one of these variants as *Terebratula pectiniformis hilseana*, but the separate name is not justified.

Another marked variant was originally described by Pusch (1836 : 24) as a variety of *Terebratula reticulata* Schlotheim and was subsequently redescribed as *Terebratula puscheana* by Roemer (1840 : 114 ; pl. 16, fig. 29). It is from the Hilsconglomerat, Berklingen, and differs from the typical *O. alemannica*, described here,

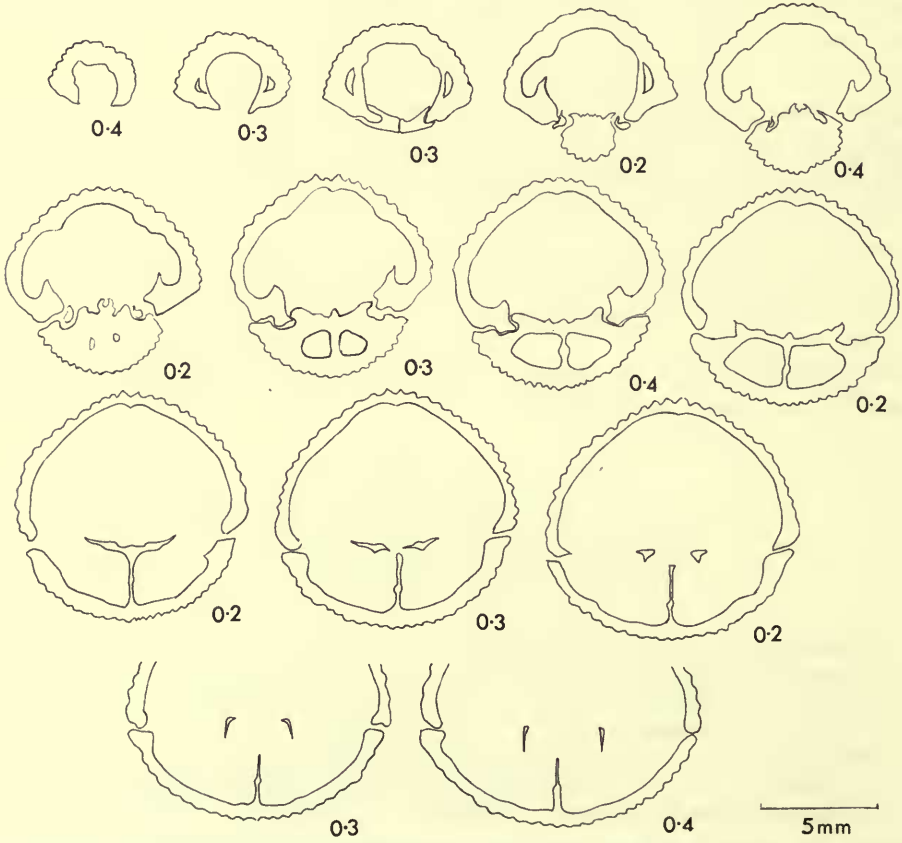

Fig. 14. Fourteen serial sections of a specimen of *Oblongarcula alemannica* sp. nov. showing the strong persistent brachial septum and elongate-triangular hinge-plates, as seen in the type species *Oblongarcula oblonga*.

in having finer radial shell ornament consisting of numerous intercalating and bifurcating costellae interrupted by well-marked concentric growth-lines. The anterior commissure of this variety is often strongly antiplicate and this feature alone might have provided sufficient reason for the two variants having been separated. There is ample evidence of human sorting in most of the collections examined.

Strombeck & von Buch (1850) figured a very convincing series of specimens (pl. 4) showing gradation from the typical oval, strongly costate form, to the almost smooth antiplicate varieties together with numerous costate and semicostate intermediate forms. All the specimens are from the Hauterivian of the Hanover–Brunswick district of north Germany. A similar series of eleven variants exists in the Davidson Collection (BM(NH) B 1200) from the Neocomian of Schoppenstedt, Germany. Specimens exhibiting intermediate characters also occur in the Lower Cretaceous, Hauterivian, of the Haute Marne, France and several examples of these are also in the Davidson Collection (BM(NH) B 6678 and B 6690).

Holotype. *Oblongarcula alemannica* sp. nov. was originally described by Roemer (1836 : 46), as *Terebratula oblonga* Sow., from the Hilsthon of the Hilsconglomerat, Elligser Brinke, near Hanover, north Germany. These beds are considered to be of Hauterivian age by present German workers. Roemer was obviously under the impression that his species was synonymous with the species previously described by J. de C. Sowerby (1829) from the Aptian of England. It would have been appropriate to choose Roemer's specimen as the holotype of *O. alemannica* but the original was lost during World War II. As holotype for *Oblonga alemannica* sp. nov., a specimen closely resembling Roemer's original is here selected from a series of five in the Hildesheim Museum, from the Hilsconglomerat of Berklingen. It has been registered as RM 756.

Remarks. The extremes of variation noted within this species are admittedly broad and such differences may be of minor stratigraphical significance. But this has still to be demonstrated and, for the time being, it would be preferable not to use more than one taxon.

O. alemannica is not uncommon in the argillaceous beds of Hauterivian age at Grenslerberg, Schoppenstedt, Berklingen and Gros Vahlberg in north Germany and also from beds of similar age and lithology at St Dizier, Haute Marne, France. Records of its occurrence in Spain and southern France have not been substantiated.

Although it is not suggested there is any direct relationship, it is interesting that a somewhat similar range of variation occurs in the Middle Liassic species *Fimbriothyris guerangeri* (Eudes-Deslongchamps) which also has an arrangement of cardinalia and brachial loop like that of *O. alemannica* (Muir-Wood 1965 : H828). Eudes-Deslongchamps (1862–85 : 23 ; pl. 23, figs 4–10) figures a series of specimens showing a full range of morphological variation, from strongly costate to polyplicate with an almost smooth shell surface, a range which is in many ways similar to that of the species described here.

Dimensions. Holotype, 18·9 mm long, 14·7 mm wide and 12·5 mm thick. Other specimens, all in the British Museum (Natural History), London, have dimensions as follows (measurements in mm).

	Length	Width	Thickness
(a), from the Haute Marne, France			
B 6678	21·5	16·1	11·0
	17·8	13·3	9·9
(b), from Schoppenstedt, north Germany			
B 12000	18·1	13·0	12·1
	16·9	11·5	10·0
	16·0	11·9	10·0
	15·9	12·1	9·4
(c), from Berklingen, near Brunswick, north Germany			
B 21920	16·8	12·1	9·9
	17·8	12·9	10·4
	15·9	10·7	7·6

Oblongarcula oblonga (J. de C. Sowerby 1829)

Figs 15–16; Pl. 2, figs 10a–c; Pl. 3, figs 1a–c.

1829 *Terebratula oblonga* J. de C. Sowerby : 68 ; pl. 535, figs 4, 5, 6.
1838 *Terebratula oblonga* Sow. ; von Buch : 159 ; pl. 16, fig. 2.
1845 *Terebratula oblonga* Sow. ; Forbes : 346.
1852 *Terebratella fittoni* Meyer ; Davidson : pl. 8, figs 8–13 [non Meyer].
1864 *Terebratula oblonga* Sow. ; Meyer : 254 ; pl. 11, figs 12–14.
1874 *Terebratella oblonga* (Sow.) Davidson : 26 ; pl. 2, figs 29–31.
1959 *Oblongarcula oblonga* (J. de C. Sowerby) Elliott : 147.

Emended description. Elongate-oval, acutely biconvex *Oblongarcula*, with numerous radiating, sharply angular costae, often deeply incised and with occasional bifurcation. Rectimarginate to incipiently uniplicate, with almost imperceptible median fold on brachial valve. Massive umbo truncated by large circular

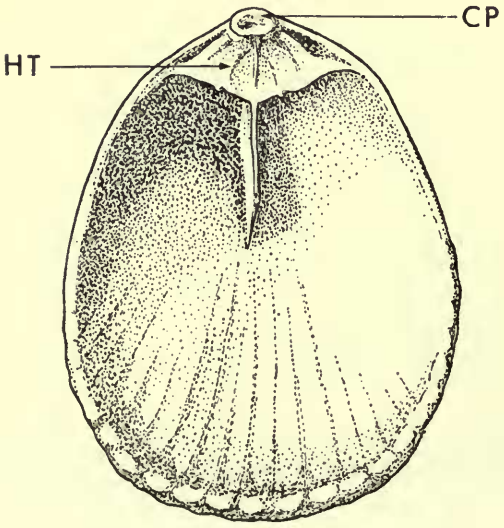

Fig. 15. Brachial valve of *Oblongarcula oblonga* (J. de C. Sowerby) from the Upper Aptian, Faringdon, Berkshire, showing the typical disc-like cardinal process CP and the broad, comparatively shallow hinge-trough HT. ×4.

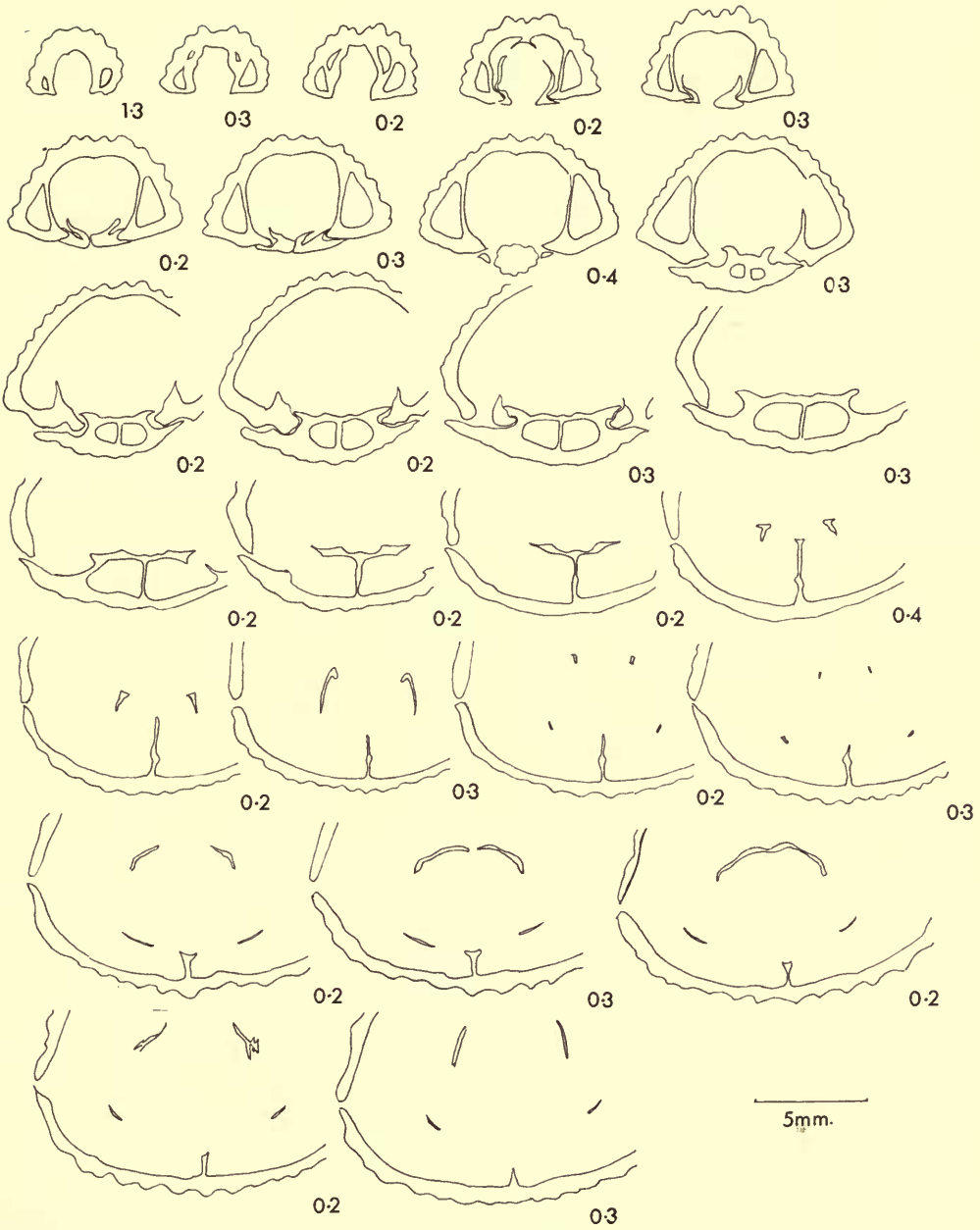

FIG. 16. Transverse serial sections through a specimen of *Oblongarcula oblonga* (J. de C. Sowerby) from the Upper Aptian, Hythe Beds, Hythe, Kent, showing the well-developed pedicle collar in the pedicle umbo and the broad, shallow hinge-trough, long triangular hinge-plates and high persistent supporting median septum in the brachial valve.

foramen. Conjunct deltidial plates well exposed. Extensive triangular interarea bordered by sharp or well-defined beak-ridges.

Internal structure shows well-defined pedicle collar situated between early-developing, slightly divergent, sub-parallel dental lamellae enclosed within callus at posterior end of pedicle valve. As seen in successive serial sections, the transversely elliptical, disc-like cardinal process develops early from the posterior extremity of the brachial umbo. A wide rectangular hinge-trough develops and extends anteriorly, becoming shallower and maintaining a broad shallow depression. The distal ends of the hinge-trough give rise to elongate-triangular hinge-plates supported by a high, persistent median septum. Massive, subquadrate hinge-teeth are deeply inserted with extensive inner and outer socket-ridges. No attachment of brachial loop to median septum noted in serial sections.

Holotype. B 61628 in the Sowerby Collection, British Museum (Natural History), London, from the Upper Aptian Sponge Gravel, Faringdon, Berkshire.

Dimensions. Holotype, 21·9 mm long, 16·5 mm wide and 13·6 mm thick. Other specimens from the same formation, all in the British Museum (Natural History), have dimensions as follows (measurements in mm).

	Length	Width	Thickness
B 25979	21·2	17·3	14
	22·4	17·1	13
	23·0	18·0	12·5
	22·6	19·0	13·7
	20·0	15·1	12·8
BB 3542	20·2	15·7	12·4
BB 3543	18·4	14·5	11·1
BB 3544	15·8	11·9	9·9

Distribution. Apart from its occurrence in the Upper Aptian Lower Greensand, at Faringdon, Berkshire, *O. oblonga* also occurs at a similar horizon in the ferruginous deposits at Seend, Wiltshire, in the Hythe Beds of the Folkestone and Maidstone districts of Kent and in the Lower Greensand, *Parahoplites nutfieldensis* Zone, at Atherfield and Shanklin, Isle of Wight. A well-marked variant occurs in the Bargate Beds at Guildford and Godalming, Surrey and in the Upper Aptian beds of Brickhill, Bedfordshire and Upware, Cambridgeshire. It differs from the typical form in its smaller size, more regular oval outline, finer and less incised costae and more obvious growth-lines.

Remarks. The relationship between *O. oblonga* and the foregoing *Oblongarcula alemannica* sp. nov., from the Hauterivian of north Germany and France, appears to be a direct one. The external morphology of the two forms is very similar and this was why Roemer (1836) assigned his specimen from the Hilsthon of Elligser Brinke to Sowerby's *Terebratula oblonga*. There are, however, certain minor differences in internal structure which should be noted. In successive sections a small amorphous calcareous structure is seen to precede the development of the hinge-plates in *O. alemannica* and occupy a vague position approximately in the centre

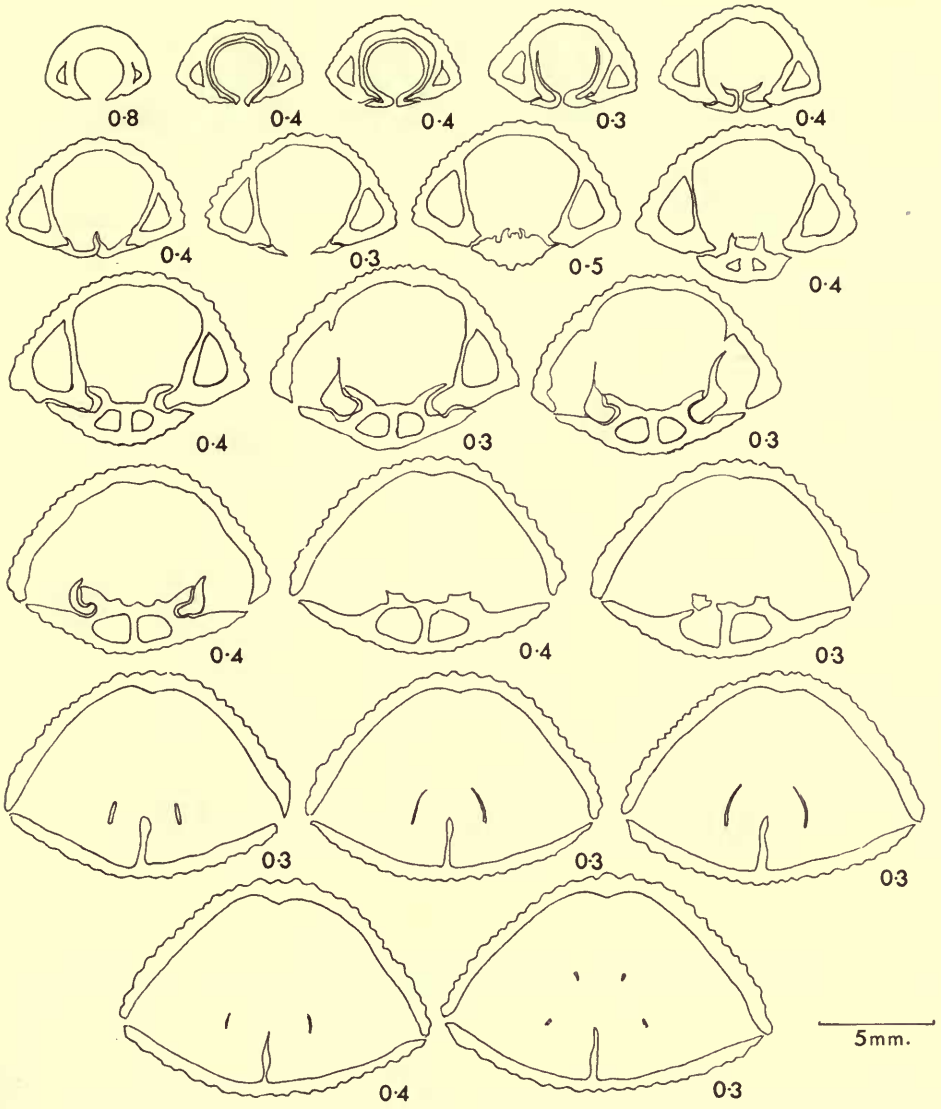

FIG. 17. *Oblongarcula davidsoni* (Walker) from the Upper Aptian of Upware, Cambridge. A series of serial sections justifying its assignment to *Oblongarcula*.

of the hinge-trough. It does not persist and soon flattens as the hinge-plates develop anteriorly.

It is probable that the species described by Walker (1867) as *Terebratella davidsoni*, from the Lower Greensand of Upware, is a further development or lateral variation of the main *oblonga* stock; it is assigned here to the genus *Oblongarcula* (Fig. 17; Pl. 3, figs 7a–c).

Genus *ARENACIARCULA* Elliott 1959

TYPE SPECIES. *Terebratella fittoni* Meyer 1864.

EMENDED DESCRIPTION. The original description given by Elliott (1959 : 147) was brief and did not mention any transverse serial sections of the type species. The emendation given here includes serial sections, Fig. 18, below, for comparison with those of *Oblongarcula oblonga* J. de C. Sowerby, Fig. 16, p. 231, and *Gemmarcula aurea* Elliott, Fig. 2, p. 212.

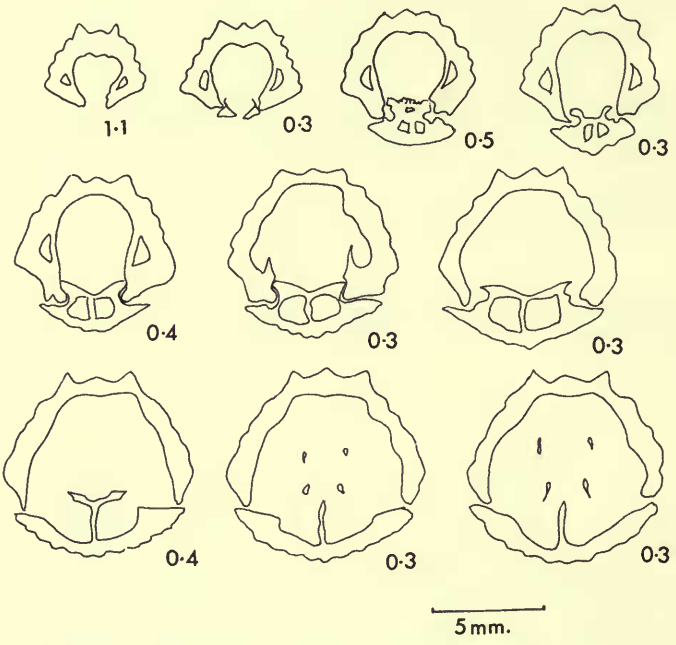

FIG. 18. A series of ten serial sections through a specimen of *Arenaciarcula fittoni* (Meyer) from the Upper Aptian of Brickhill, Buckinghamshire.

The sections show that the test of *Arenaciarcula* is thicker than in either *Gemmarcula* or *Oblongarcula* and that the cardinal process is more highly developed. The dental lamellae appear to be stronger or more persistent in *Arenaciarcula* and the median septum, which supports the hinge-plates in the same way as is seen in *Oblongarcula*, breaks away much more quickly, leaving thick, comparatively shorter, triangular hinge-plates to form the crural bases and to develop long crural processes ventrally. The septum persists anteriorly for over two-thirds of the length of the valve and must have formed a firm point of attachment for the brachial loop in earlier developmental stages. No attachment of brachial loop to septum appears in any of the serial sections so far examined.

RANGE. Upper Aptian to Middle Cenomanian.

Arenaciarcula fittoni (Meyer 1864)

Figs 18, 19; Pl. 2, figs 8a–c.

1836 *Terebratula quadrata* J. de C. Sowerby in Fitton : pl. 16, fig. 9.
1864 *Terebratella fittoni* Meyer : 250 ; pl. 11, figs 1–10.
1872 *Terebratula* (*Terebratella*) *fittoni* Meyer ; Pictet : 129 ; pl. 207, fig. 2a–c.
1874 *Terebratella fittoni* Meyer ; Davidson : 26 ; pl. 8, figs 8–13.

DESCRIPTION. Although adequately described by Meyer (1864), a certain amount of confusion has arisen between this species and *Oblongarcula oblonga* (J. de C. Sowerby). To a certain extent this is understandable, since the two forms have much in common. They are both comparatively small oval species with sharp, suberect beaks, well-marked beak-ridges and strong radiating costae. A more critical examination of both forms reveals that *A. fittoni* is more uniform in size and outline. It has a fairly well-marked, but not highly developed, median fold in the brachial valve and sometimes a faint corresponding sulcus in the pedicle valve. It is also narrower and more acutely biconvex than *Oblongarcula oblonga.*

Meyer stated in the original description (1864 : 250) that the species could be 'distinguished from *T. oblonga* by its diminutive size and by the smaller number and inequality of the ribs.' It also has a more highly developed cardinal process and a shorter, more acutely triangular and deeper hinge-trough.

TYPE SPECIMEN. Some of Meyer's material can be found among the Davidson Collection in the British Museum (Natural History), but no specimens which might have been designated type or which Meyer might have used in the original description of *T. fittoni* have been found. It is still possible that his original specimen may be found among the collections of the Sedgwick Museum, Cambridge or in the general collections of the BM(NH), and so the question of designating a neotype for the species should remain for the time being.

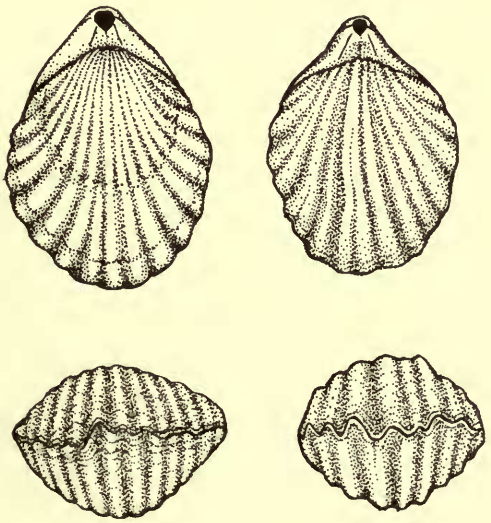

FIG. 19. Diagram of two specimens of *Arenaciarcula fittoni* (Meyer) from the Upper Aptian of Brickhill, Buckinghamshire, showing variation in general outline, beak characters, costae and anterior commissure. × 3.

Distribution. *Arenaciarcula fittoni* appears to be confined to beds within the Upper Aptian and is found in the Lower Greensand at Upware, Cambridge and at the same horizon at Brickhill, Buckinghamshire. It also occurs in the Bargate Pebble Bed at Tewsley, Guildford, and Godalming, Surrey, from where it was originally described by Meyer, and also from the Upper Aptian at Maidstone and Sevenoaks, Kent. A specimen figured by Pictet (1872 : pl. 207, fig. 2a–c) was accompanied by a brief description but no locality was given. From its appearance it almost certainly originated from England and was probably presented to Pictet by Meyer.

Remarks. Confusion with *O. oblonga* may have created a wrong impression regarding its occurrence. The species is, in fact, comparatively rare. Although often found in association with *O. oblonga*, it seems to have been more rigidly controlled by ecological conditions.

Arenaciarcula beaumonti (d'Archiac 1847)

Fig. 20 ; Pl. 2, figs. 7a–c.

1847 *Terebratula Beaumonti* d'Archiac : 331 ; pl. 21, figs 12–14.
1852 *Terebratula oblonga* Sow. ; Davidson : 51 ; pl. 2, figs 32, 32a–b.
1867 *Terebratula* (?) *Beaumonti* d'Archiac ; Schloenbach : 461 ; pl. 22, figs 3–5.
1869 *Trigonosemus kiprijanovi* Hofman : 25 ; pl. 5, figs 18–21.
1871 *Terebratula orbicularis* Sow., Quenstedt : 293 ; pl. 45, figs 63–69.
1874 *Terebratella Beaumonti* (d'Archiac) Zareczny : 177 ; pl. 2, fig. 2.
1916 *Terebratella Beaumonti* (d'Archiac) ; Ravn : 22 ; pl. 4, fig. 8.
1969 *Terebratella beaumonti* (d'Archiac) ; Panow : 593 ; pl. 112, fig. 5.
1972 *Oblongarcula beaumonti* (d'Archiac) Popiel-Barczyk : 127 ; pl. 1, figs 1–5 ; pl. 4, fig. 3.

Description. D'Archiac's species has been recently reviewed and described by Popiel-Barczyk (1972 : 127), who gave a series of serial sections (: 130–133) and reconstructed the brachial loop of a specimen from the Cenomanian of Annopol, Poland. The transverse serial sections of *Arenaciarcula acuticostata* sp. nov., Fig. 21, p. 239, can be compared with these. At present nothing need be added to her definitive account.

Both series of sections show the typical bifid cardinal process with additional thickened myophore extension. This structure occupies an area just inside the pedicle umbonal cavity and in successive sections remains fairly well defined, with the development of steep-sided inner and outer socket-ridges. The hinge-trough is, therefore, deep and subquadrate in transverse outline. The hinge-plates are elongate-triangular and remain supported by the septum from the floor of the brachial valve for a comparatively short distance. This distinguishes it from the true *Oblongarcula* where the median septum supports the fused hinge-plates for a greater distance into the valve.

Material. Eleven specimens from English and European localities have been measured and are listed below. In addition there are two poorly-preserved internal moulds (B 40411) from Galicia, Austria, which are recognizable as typical forms.

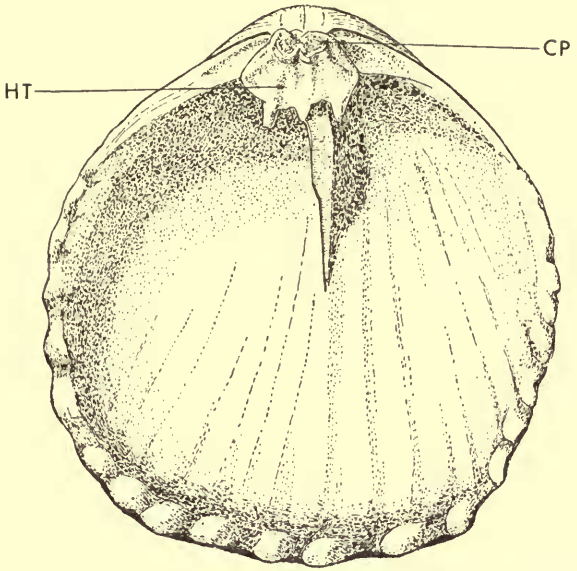

FIG. 20. Brachial valve of a specimen of *Arenaciarcula beaumonti* (d'Archiac) from the Tourtia of Tournai, Belgium, showing the comparatively well-developed bifid cardinal process CP and hinge-trough narrower than in *Oblongarcula*. × 4.

All the specimens are in the general collections of the British Museum (Natural History) (measurements in mm).

	Length	Width	Thickness
(a), from the middle Cenomanian Limestone, Wilmington, Devon			
BB 45977	10·7	9·0	7·6
BB 45978	9·2	8·0	6·2
BB 45979	10·0	8·0	7·0
(b), from the Tourtia of Tournai, Belgium			
B 35502	11·9	9·0	8·0
	11·0	8·9	7·9
	10·0	8·1	7·1
	10·0	9·0	6·2
	11·1	10·0	7·4
	10·0	8·0	6·0
	8·7	8·0	6·0
(c), from Essen, north Germany			
B 35684	9·9	7·9	6·0

REMARKS. In removing this species from the genus *Oblongarcula* into which it had somewhat tentatively been placed by Popiel-Barczyk (1972), I have no doubts that it should be classified with *Arenaciarcula fittoni* and *A. acuticostata* sp. nov., although no reconstructions of the loop structures have been prepared from serial sections.

Schloenbach (1867 : pl. 22, fig. 3e) shows a brachial valve of a specimen with exposed loop having a point of attachment to the septum at approximately mid-point of the valve. His fig. 5 shows a slightly reconstructed valve and loop with attachment bands of loop to septum and elongated lateral spurs or 'flanges' on the transverse band of the loop. These illustrations confirm the descriptions and reconstructions, showing similar lateral spurs, given by Popiel-Barczyk (1972 : 131).

The species is more widespread geographically than some of its associated fauna and occurs, as stated, in the Tourtia of Belgium, the same horizon in the Essen Greensand of north Germany, the Cenomanian of Annopol, Poland and Russia, in the basal conglomerate on Bornholm, Denmark and in the Cenomanian Limestone of Wilmington, Devon. A similar species, although not regarded here as conspecific, was described by Vantschurov (1966 : 110 ; figs 3, 4) from the Cenomanian of Turkmenistan as *Trigonosemus kamyschalaensis*. From the associated transverse serial sections, the species is clearly congeneric with *A. beaumonti* and is referred here to *Arenaciarcula*.

Although bearing a superficial resemblance to *Oblongarcula oblonga*, *Arenaciarcula beaumonti* can be distinguished by its more acutely biconvex outline, deeply incised radiating costae very rarely bifurcating, its narrower hinge-line and constant rectimarginate anterior commissure. The internal structures differ in their cardinalia and loop morphology.

Arenaciarcula acuticostata sp. nov.

Fig. 21 ; Pl. 2, figs 6a–c.

1903 *Terebratella hercynica* (Schloenbach) Walker : 257 ; pl. 18, fig. 4a–c (non Schloenbach).

Diagnosis. Acutely biconvex *Arenaciarcula*, triangular in general outline. Average length 17 mm, width 14 mm and thickness 13 mm. Costae sharp, deeply incised. Umbo slightly produced, beak suberect. Beak-ridges sharp ; interarea short. Anterior commissure rectimarginate.

Description. This species was originally described by Walker (1903 : 257) as *Terebratella hercynica* (Schloenbach), from the Lower Albian of Leighton Buzzard, Bedfordshire. Walker confused his specimen with the species described and figured by Schloenbach (1867 : 467 ; pl. 22, figs 6, 7) from the Cenomanian of Laugenberges near Quedlinburg, north Germany. The two species are, however, quite distinct and are assigned to different genera on the grounds of their internal structures.

The serial sections of *A. acuticostata* given here (Fig. 21) have been compared with those made from duplicate specimens of *Arenaciarcula beaumonti* (d'Archiac) from the Tourtia of Tournai, Belgium, and may also be compared with a similar series presented by Popiel-Barczyk (1972 : 130) for a specimen of *A. beaumonti* (d'Archiac) (under the name of *Oblongarcula beaumonti*) from the Cenomanian of Annopol, Poland. It will be seen that the two forms have generally similar cardinal processes and cardinalia, with the same or similar arrangement of hinge teeth and hinge-plate extensions. It will also be seen that the two species have similar triangular hinge-plates which, although initially fused, are not supported for a great

distance by the median septum of the brachial valve and soon break away with the development of the crural bases and descending branches of the loop. The branches themselves remain fairly close to the septum, a character noted in serial sections of *Terebrirostra* and *Dereta*.

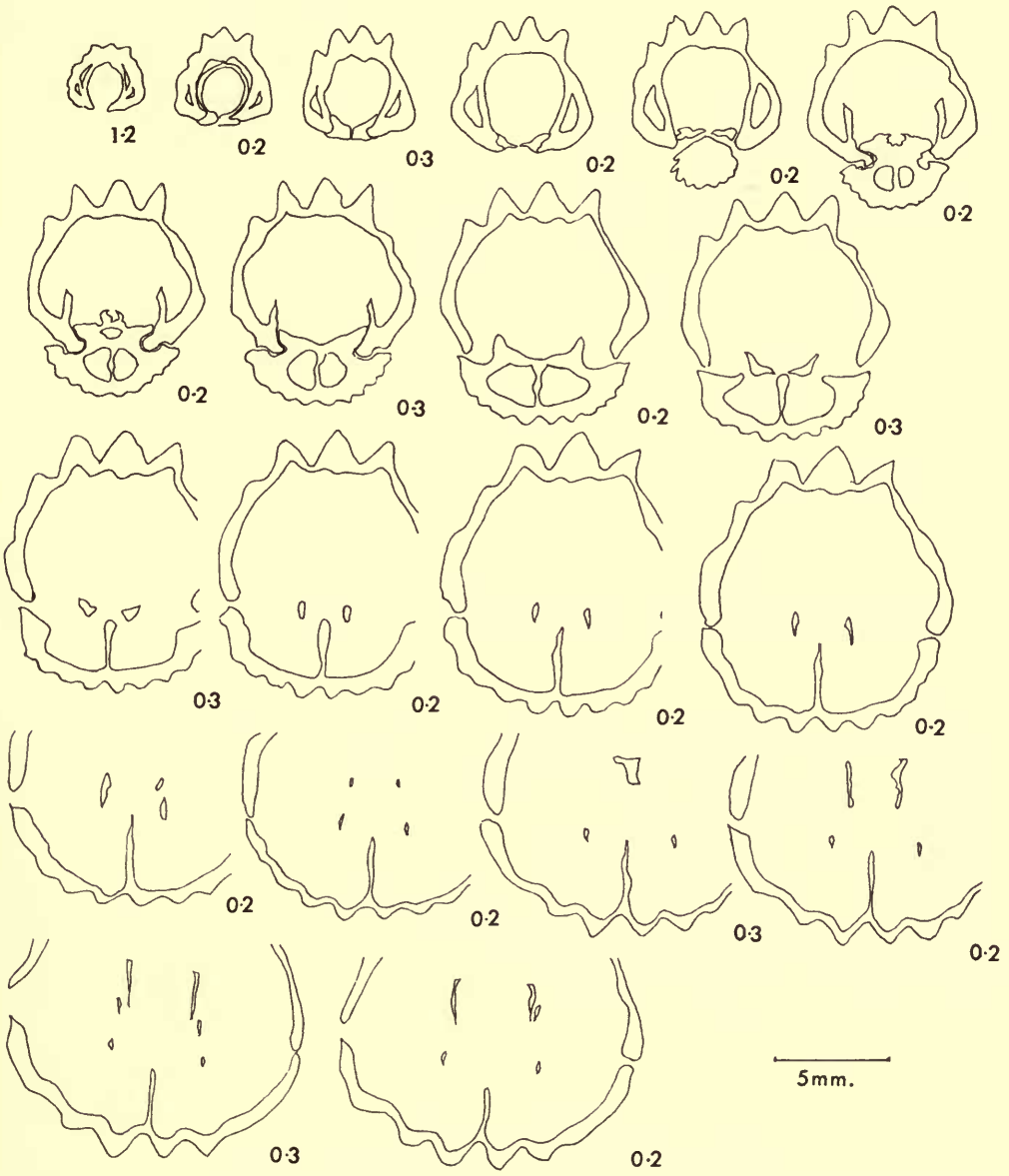

FIG. 21. *Arenaciarcula acuticostata* sp. nov. from the Lower Albian, Leighton Buzzard, Bedfordshire. A series of serial sections which can be compared to those of *A. beaumonti* (d'Archiac) from the Cenomanian of Annopol figured by Popiel-Barczyk (1972).

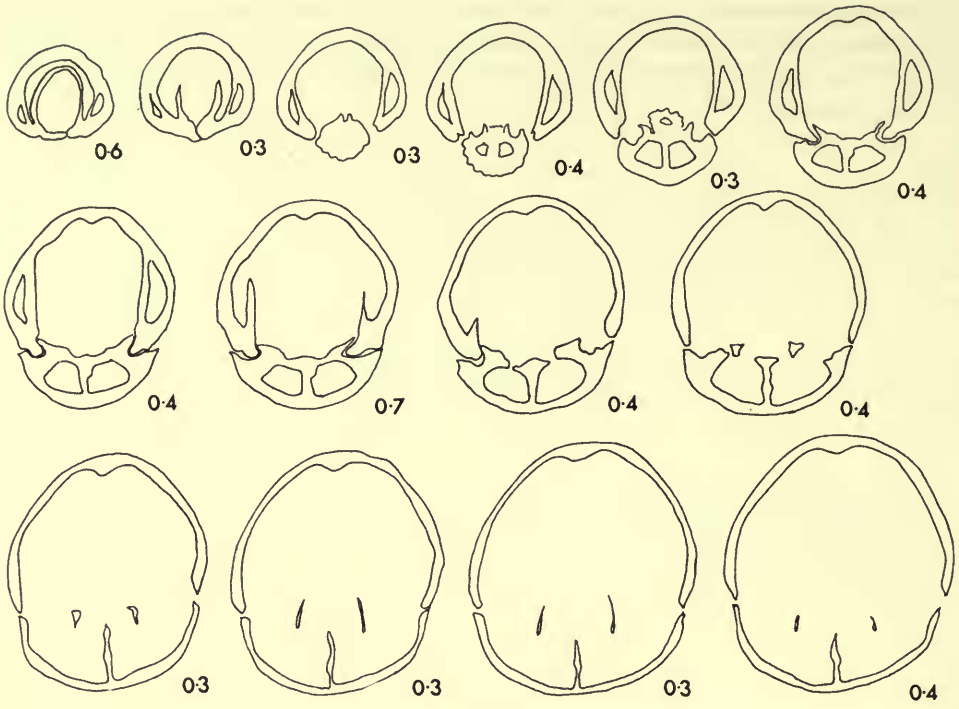

FIG. 22. Transverse serial sections of a specimen of *'Terebratella' keepingi* Walker from the Upper Aptian of Brickhill, Buckinghamshire. The species is somewhat tentatively assigned to *Arenaciarcula*. (See Pl. 3, fig. 3).

HOLOTYPE. The specimen described and figured by Walker (1903 : 257 ; pl. 18, fig. 4a–c) as *Terebratella hercynica* (Schloen.) and now in the collections of the Institute of Geological Sciences, London, registered as GSM 51275, is chosen as holotype of *Arenaciarcula acuticostata* sp. nov. Dimensions : length 16·6 mm, width 14·2 mm and thickness 13·0 mm.

REMARKS. The species appears to be confined to the Lower Albian of Shenley Hill and other localities in the Leighton Buzzard district. Smirnova (1972 : pl. 9, fig. 2), however, figured a specimen from the Upper Albian of the Tekedzhik, Turkmenistan SSR, as *Eudesia tekedgikensis* ; it bears a very strong resemblance to *Arenaciarcula acuticostata* sp. nov., but no serial sections were given.

Family **TEREBRATELLIDAE** King 1850
Subfamily **TRIGONOSEMINAE** Elliott 1965
Genus ***TRIGONOSEMUS*** Koenig 1825

TYPE SPECIES. *Trigonosemus elegans* Koenig 1825.

Trigonosemus elegans Koenig 1825

Figs 23, 24; Pl. 3, figs 2a–c.

1825 *Trigonosemus elegans* Koenig : 3 ; pl. 4, figs 73a–e.
1848 *Fissurirostra elegans* d'Orbigny : 134 ; pl. 520, figs 9–13.
1848 *Fissurirostra pectita* d'Orbigny : 136 ; pl. 520, figs 14–18.
1848 *Fissurirostra recurva* d'Orbigny : 133 ; pl. 520, figs 1–8.
1852 *Trigonosemus elegans* Koenig ; Davidson : 29 ; pl. 4, fig. 3.

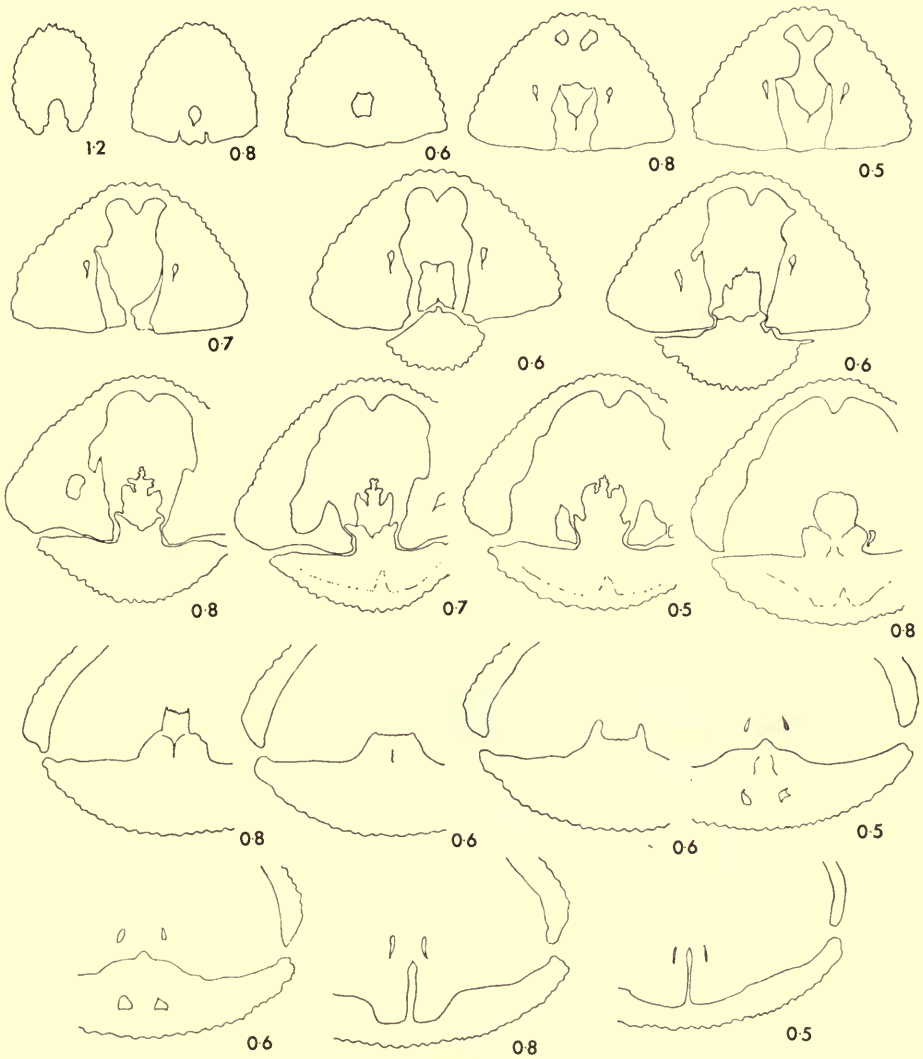

FIG. 23. A series of 19 serial sections through a specimen of *Trigonosemus elegans* Koenig from the Upper Chalk of Ciply, Belgium. This shows the extraordinary shell thickening and highly developed trifid cardinal process and semisphaeroidal cardinal bulge occupying the shallow hinge-trough.

EMENDED DESCRIPTION. *Trigonosemus*, elongate-oval to broadly pentangulate, averaging 22 mm in length, 21 mm in width and 17 mm in thickness. The pedicle umbo is broad and produced with a slightly incurved, acutely pointed beak. The beak-ridges are sharply defined and border a wide, extensive interarea. The permesothyridid foramen is small and circular in outline. Well-developed, faintly striate symphytium with conjunct deltidial plates. Anterior commissure sulco-carinate to elliptical in transverse outline. The shell surface is ornamented with approximately 50–55 rounded costellae with a tendency to bifurcation.

Internal structure. *T. elegans* is typified by a highly developed cardinal process, just anterior to the base of the trifid lobes of which is a semisphaeroidal bulge, similar in many respects to the thickened base of the cardinal process seen in *Pachymagas* and *Neothyris* from the Tertiary. This bulge usually occupies most of the area of the hinge-trough and is fused anteriorly with the hinge-plates. Other species within the genus, such as *T. pectiniformis* von Buch (Fig. 25 ; Pl. 1, figs 7a–c) and *T. palissyi* Woodward (Fig. 26), do not appear to have such advanced development of this character, although they have many of the other generic features.

In a description of *Trigonosemus pulchellus* Nilsson, Steinich (1965:176) illustrates altogether different cardinalia. His specimen is shown to have a produced posterior rim or ridge to the hinge-trough, with a centrally-developed low cardinal process which is divided longitudinally by a short, poorly-defined septum. This type of

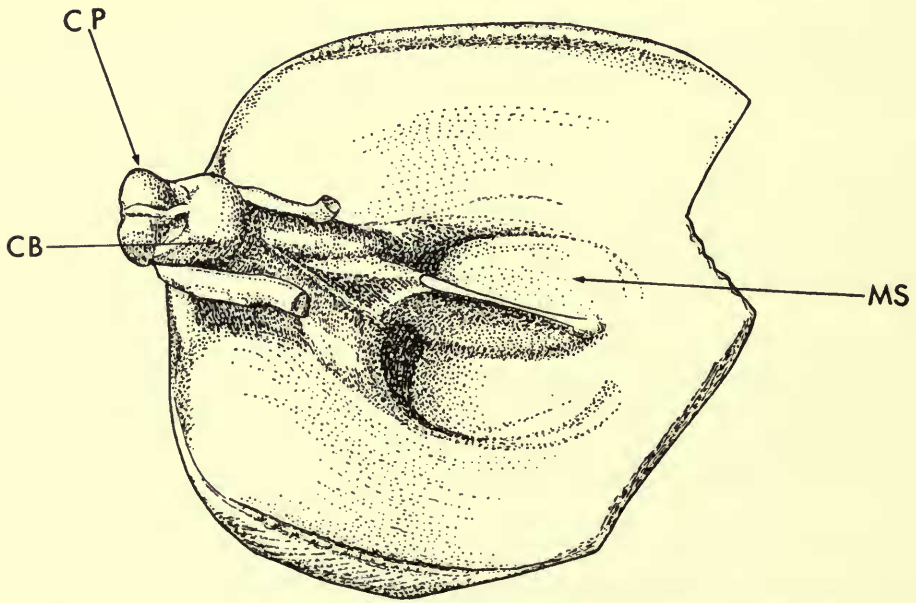

FIG. 24. The produced and highly developed trifid cardinal process CP and semisphaeroidal cardinal bulge CB are characters which distinguish *Trigonosemus elegans* Koenig from any other terebratellacean within the Cretaceous. The deeply sunken muscle-scars MS are also distinctive but not necessarily of generic importance. ×4.

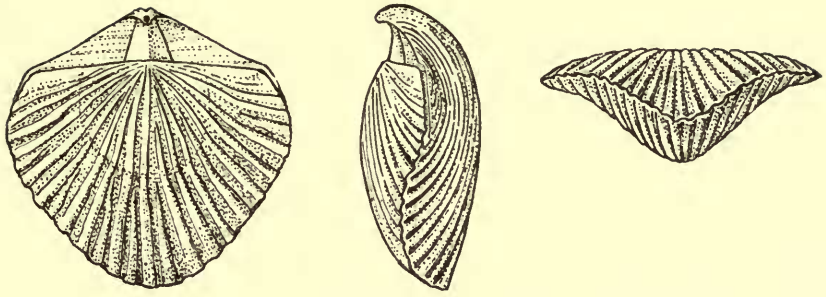

FIG. 25. Although assigned to the genus *Trigonosemus*, *T. pectiniformis* (von Buch) shows few of the external generic characters. It has differently shaped costae, which show fairly frequent intercalation, and has a well-marked anterior sulcus in the brachial valve. × 3.

cardinalia is so atypical of the genus *Trigonosemus* as to suggest that further investigation of the types and topotype material is needed. It may be found that *T. pulchellus* represents an undescribed line of development closely related to *Trigonosemus*.

The brachial loop of *T. elegans* is rarely preserved intact, but sufficient information has been obtained from broken loops to be reasonably certain that it is of a terebratellid development.

LECTOTYPE. Koenig did not indicate or designate any type material and the exact locality of his illustrated specimens (1825 : pl. 4, figs 73d, e) is not known. Within the general collections of the British Museum (Natural History) are two specimens from the S. P. Woodward Collection collected from the *Baculites* Zone

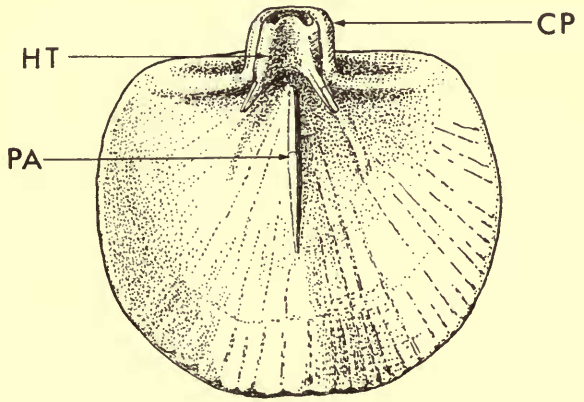

FIG. 26. *Trigonosemus palissi* (Woodward), from the Ciply Chalk, also departs from the typical form in having a completely different type of cardinal process, CP, which is shown as an elongation or posterior extension of the rim of the hinge-trough HT. The point of attachment of the brachial loop is approximately in the same position as in *Ruegenella* gen. nov. × 4.

of the Maastrichtian, near Caen, France. They comprise a brachial and a pedicle valve which resemble those figured by Koenig. Furthermore, Koenig was employed as curator of the fossil collections at the British Museum at the time the specimens were described and figured. G. R. Waterhouse has left an authoritative testament, recorded on the label of the subsequently curated valves, indicating that these were in fact the specimens figured by Koenig. One of these, the brachial valve, fig. 73d, is registered as B 81568, and is here selected as lectotype of the species *Trigonosemus elegans* Koenig 1825. Dimensions : length 17·9 mm, width 20·0 mm.

Remarks. *Trigonosemus elegans* is a comparatively rare fossil occurring in the Upper Chalk, Maastrichtian, Ciply, Belgium and at the same horizon in Holland, as well as at the type locality near Caen, Normandy, France.

In Britain, specimens assigned to *Trigonosemus elegans* have been found in the Upper Senonian of Norwich, Norfolk and in Chalk detritus at Charing, Kent. The Kentish specimen, figured by Davidson (1852 : pl. 4, fig. 3), is flatter and considerably smaller than the typical form and, although obviously congeneric, may not belong to the type species *T. elegans*.

Dimensions. Other specimens from the Maastrichtian of Ciply, Belgium, all in the British Museum (Natural History), have dimensions as follows (measurements in mm).

	Length	Width	Thickness
BB 45974 (Pl. 3, figs 2a–c)	27·1	23·1	16·0
B 35508	28·0	21·5	18·2
	28·0	23·6	17·0
	25·0	21·4	14·8
	27·0	23·0	16·2
B 46338	23·1	21·6	12·2
B 46340	24·0	21·6	14·5
B 46341	26·3	25·0	15·2
	16·8	15·0	8·2

Genus ***TEREBRIROSTRA*** d'Orbigny 1850

Type species. *Terebratula lyra* J. Sowerby 1816.

Terebrirostra arduenensis d'Orbigny 1850

1850 *Terebrirostra arduenensis* d'Orbigny : 128 ; pl. 519, figs 60, 61.
1872 *Terebratula* (*Terebrirostra*) *arduenensis* d'Orbigny ; Pictet : 132 ; pl. 207, fig. 13.
1903 *Terebrirostra lyra* (Sow.) var. *incurvirostrum* Walker : 255 ; pl. 18, figs 1a–b, 2a–b.
1934 *Terebrirostra incurvirostrum* Lamplugh & Walker ; Muir-Wood : 554 ; fig. 14.

Description. The original description by d'Orbigny (1850 : 128) and the additional description given by Pictet (1872 : 132) are adequate for the species, but the internal structure of the genus was not fully understood until Muir-Wood (1934 : 553) figured a series of transverse serial sections through the umbo of a specimen of the type species *T. lyra* (J. Sowerby) from the Cenomanian of Warminster, Wiltshire.

She used this information to compare with the internal structures seen in a series of longitudinal sections (1934 : fig. 14) through a specimen of *Terebrirostra incurvirostrum* Walker from the Lower Albian of Shenley Hill, Leighton Buzzard, Bedfordshire. Muir-Wood's serial sections illustrate the extraordinary length of the dental lamellae which originate from the extreme posterior end of the produced pedicle umbo and show the trifid cardinal process and extended hinge-plates protruding into the pedicle umbonal cavity.

The hinge-plates develop directly from a short, shallow hinge-trough, their distal ends giving rise to the descending branches of the brachial loop which remain close to the median septum, broadening anteriorly. The general arrangement of the cardinalia and shape of the hinge-plates is very similar, although not identical, to those of *Dereta* (Fig. 29, p. 248). It is probable that both genera have been developed from the same original stock, possibly related to a late Jurassic or early Cretaceous genus not yet investigated. The similarity is enough to suggest that *Terebrirostra* should be assigned to the same subfamily as *Dereta*, i.e. Trigonoseminae.

TYPE SPECIMEN. The two specimens figured by d'Orbigny (1850 : pl. 519) were collected by Raulin and Buvignier. Buvignier's collection has not been traced and no specimens remotely like this species have been found in the Raulin Collection at the École des Mines, Paris. The selection of a possible neotype for the species, therefore, is still to be considered.

DISTRIBUTION. The type locality (d'Orbigny 1850) is in the Lower Albian beds of Grandpré, northeast of the Paris Basin, France, where, according to Peron (1905), it also occurs in the Upper Aptian 'sables ferrugineux'. As this information appears to have been obtained from mine workings, however, there is always the possibility of confusion over the horizon. The species also occurs in the Lower Albian

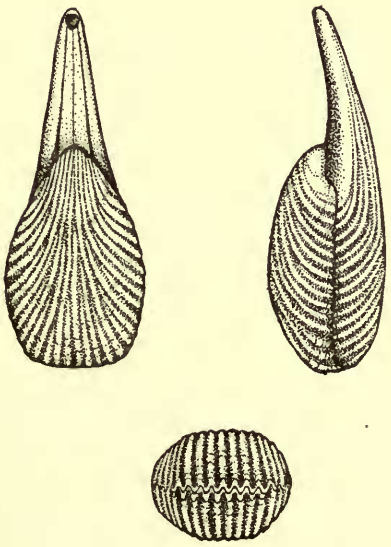

FIG. 27. The extraordinary extension of the umbo in *Terebrirostra* is a major point of distinction for the genus. The internal structures, as shown in the transverse serial sections (Fig. 28), can nevertheless be compared to those of *Dereta pectita* (Fig. 29). × 1⅓.

Leymeriella tardifurcata Zone of the Shenley Limestone at Leighton Buzzard, Bedfordshire, where it was described by Walker (1903) as *Terebrirostra lyra* var. *incurvirostrum*.

Remarks. Many of the brachiopod species described by Walker (1903) from the Shenley Limestone cannot be readily distinguished from species occurring in beds of equivalent age in the Lower Albian facies of Granpré and at Mont Saxonet, Perte du Rhône, Goudinière and Reposoir in the Haute Savoie, France. These include rhynchonelloid species and other terebratuloids and terebratelloids. Casey (1961) regarded the two species *T. arduenensis* and *T. incurvirostrum* as synonyms, but made no direct comparison of the two species with regard to the finer aspects of their morphology. We should remember there are certain minor differences in the general outline and costation of the two forms.

Genus ***DERETA*** Elliott 1959

Type species. *Terebratella pectita* (J. Sowerby 1816).

Dereta pectita (J. Sowerby 1816)

Fig. 29; Pl. 1, figs 8a–c.

1816 *Terebratula pectita* J. Sowerby : 83 ['87']; pl. 138, fig. 1.
1819 *Terebratula pectita* Sow.; Lamarck : 255.
1822 *Terebratella pectita* (Sow.) Brongniart & Cuvier : pl. 9, fig. 3.
1838 *Terebratula pectita* Sow.; von Buch : 168; pl. 16, fig. 12.
1848 *Terebratella pectita* (Sow.); d'Orbigny : 120; pl. 517, figs 16–20.
1852 *Terebratella pectita* (Sow.); Davidson : 26; pl. 3, figs 29–33.
1871 *Terebratula pectita* Sow.; Quenstedt : 267; pl. 44, figs 104–5.
1959 *Dereta pectita* (J. Sowerby) Elliott : 147.

Description. The species is variable, some forms developing a faint fold on the brachial valve with a corresponding sulcus in the pedicle valve. When these features occur with an extension of the hinge-line and more marked costae, it is very difficult to distinguish it from *Gemmarcula menardi* (Lamarck) with which it is sometimes associated. *Dereta pectita* remains subcircular in outline and is always more acutely biconvex than *G. menardi*. The costae, which are more numerous in *D. pectita*, are less deeply incised and appear more rounded in cross-section. They are given to more frequent bifurcation than in *G. menardi*, a feature which is more apparent at the margins.

The average length of the adult of the species is approximately 18 mm, width 17 mm and thickness 11 mm.

The dental lamellae in the pedicle valve appear early in development and remain strongly divergent, supporting subquadrate hinge-teeth. The cardinalia are well developed, extending into the the pedicle umbonal cavity in the early stages and gradually flattening. At the distal end of the cardinal process two plates develop and extend into the pedicle umbo, replacing the massive cardinal process. These plates are outward extensions of the hinge-plates which are fused anteriorly and

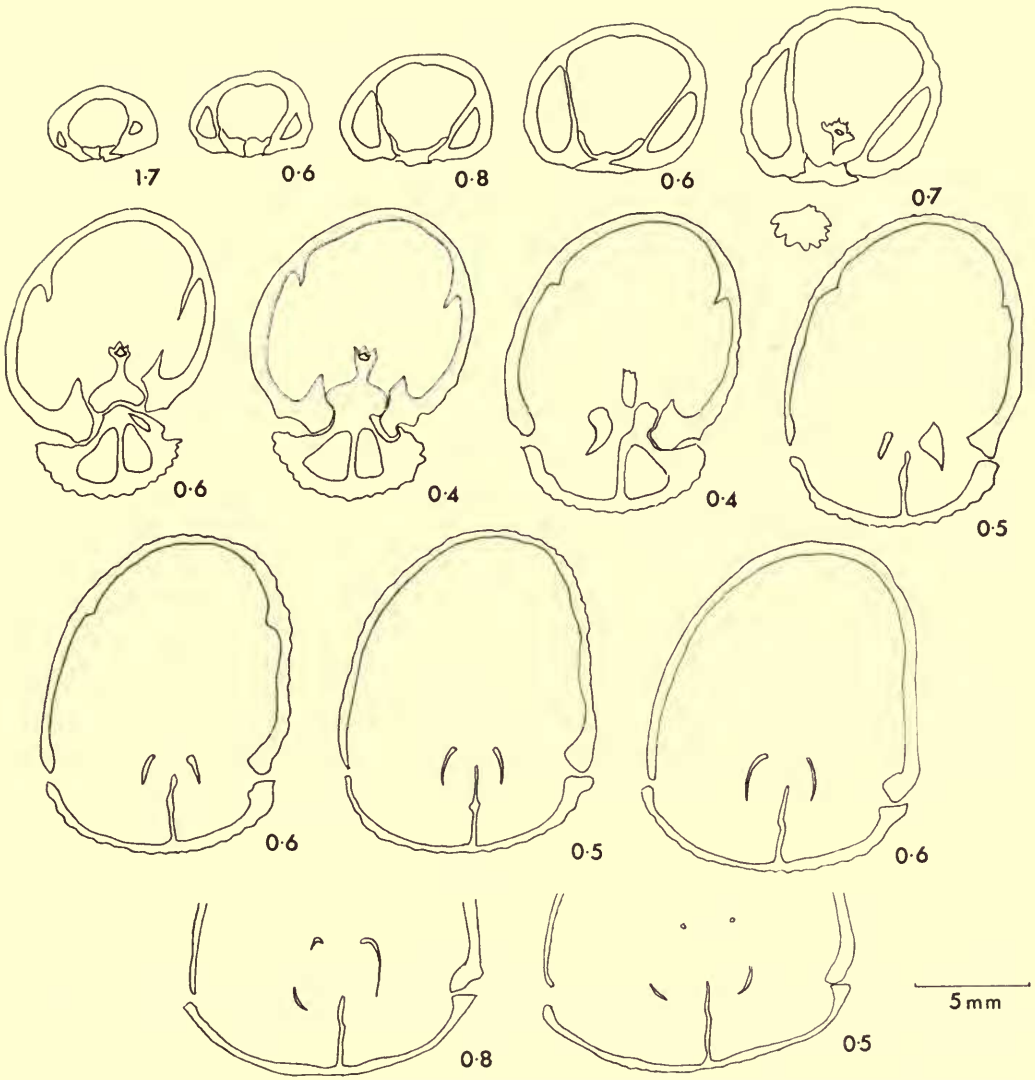

FIG. 28. Serial sections of *Terebrirostra bargesana* d'Orbigny show subtle points of distinction between this genus and *Dereta* (Fig. 29). Both series show similar extensions of the hinge-plates and poorly-developed hinge-trough. They also have a similar brachial loop pattern.

supported by a high persistent median septum from the floor of the brachial valve. The distal ends of this structure give rise to the descending branches of the brachial loop which remain close to the septum, elongating anteriorly to produce comparatively long crural processes.

HOLOTYPE. The specimen from the Upper Greensand of Horningsham, Wiltshire, in the Sowerby Collection, British Museum (Natural History), (B 61622)

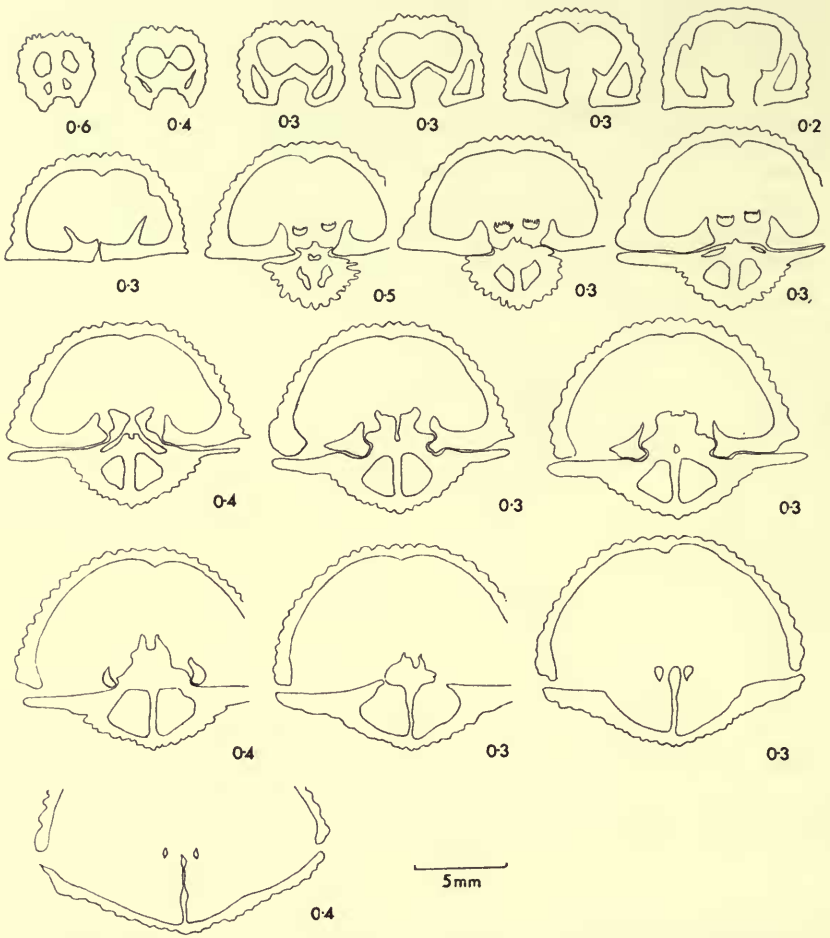

Fig. 29. *Dereta pectita* (J. Sowerby) seen in a series of 17 transverse sections. A well-marked pedicle collar, fused hinge-plates and high persistent median septum are clearly shown.

figured by J. Sowerby (1816: pl. 138, fig. 1). Dimensions: length 19·9 mm, width 20·0 mm and thickness 14·0 mm.

Distribution. Apart from the type locality near Warminster, Wiltshire, occurrences have been recorded from the Cenomanian Glauconitic Marl of Woody Bay, Binnell Point, Rocken End, Watershoot Bay and Compton Bay on the Isle of Wight, as well as from the Cenomanian Basement Bed of Swanage, Evershot and Melcombe Bingham in Dorset. Specimens have also been collected from the Upper Albian, *dispar* Zone, at Punfield Cove, Dorset.

In Europe the species appears to be confined to the Lower and Middle Cenomanian limestones of the Normandy coast, France.

Remarks. In many ways *Dereta* and *Terebrirostra* have much in common. They share a similar geographical distribution and occur in very much the same lithologies, although not always together. They have very similar internal structures but may be distinguished by certain fundamental differences in the type of cardinal process. In *Dereta* this structure consists of a fusion of two separate parts, whereas in *Terebrirostra* it has been formed by the fusion of three distinct parts, as shown in the serial sections of the type species *T. lyra* given by Muir-Wood (1934 : 553) and the series shown here, Fig. 28, for *T. bargesana* (Pl. 3, figs 4a–c) from southern France. The extraordinary elongation of the umbo in *Terebrirostra* is also regarded as a point of distinction between the two genera.

Dereta can be distinguished from *Gemmarcula* in having a more highly complex and developed cardinal process, more clearly defined and persistent dental lamellae, and a more persistent and higher median septum.

IV. ACKNOWLEDGEMENTS

I am once again indebted to the Keeper of Palaeontology, British Museum (Natural History), for permission to work on the material in his charge and I am particularly grateful for the helpful discussion and kindness of Dr G. F. Elliott, Deputy Keeper of the same Department.

My thanks are also due to Mr C. J. Wood, Institute of Geological Sciences, for helpful suggestions and loan of material, and to my colleagues at the British Museum (Natural History), Drs L. R. M. Cocks and C. H. C. Brunton, for helpful suggestions and friendship ; to Angela Foster for help with the references and for technical aid ; to Mrs Eva Wilson for the drawings in Figs 1, 6, 7, 9, 11, 12, 15, 20, 24, 26 and 28 ; to Miss Mandy Holloway for the drawings in Figs 19 and 27 ; and to Mr T. W. Parmenter for the photographic work.

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VI. INDEX

New taxonomic names and the page numbers of the principal references are printed in **bold** type. An asterisk (*) denotes a figure.

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Accepted for publication 14 July 1976

PLATE 1

All specimens in Dept. of Palaeontology,
British Museum (Natural History).
a. Dorsal view. b. Lateral view. c. Anterior view.

Gemmarcula carantonensis (d'Orbigny) (p. 217)

FIGS 1a, b, c. Upper Cenomanian, Port des Barques, Charente, France. BB 45960. × 2.

Gemmarcula menardi (Lamarck) (p. 215)

FIGS 2a, b, c. Middle Cenomanian, near Le Mans, Sarthe, France. BB 35152. × 2.

Gemmarcula aurea Elliott (p. 211)

FIGS 3a, b, c. Upper Aptian, Sponge Gravel, Little Coxwell Pit, Faringdon, Berkshire. BB 45961. × 2.

Gemmarcula trifida (Meyer) (pp. 211, 217)

FIGS 4a, b, c. Upper Aptian, Brickhill, Bletchley, Buckinghamshire. BB 45962. × 2.

Ruegenella ciplyensis gen. et sp. nov. (p. 227)

FIGS. 5a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45963. × 2.

Gemmarcula asteriana (d'Orb.) (pp. 214, 224 ; see also Pl. 2, figs 9a–c)

FIGS 6a, b, c. Aptian, Auxerre, Yonne, France. BB 45964. × 2.

Trigonosemus pectiniformis (von Buch) (p. 242)

FIGS 7a, b, c. Upper Chalk, Maastrichtian, Maastricht, Netherlands. BB 45965. × 2.

Dereta pectita (J. Sowerby) (p. 246)

FIGS 8a, b, c. Middle Cenomanian, Warminster, Wiltshire. B 25263. × 2.

Ruegenella corneti (Hanstein) (p. 225)

FIGS 9a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45966. × 1·5.

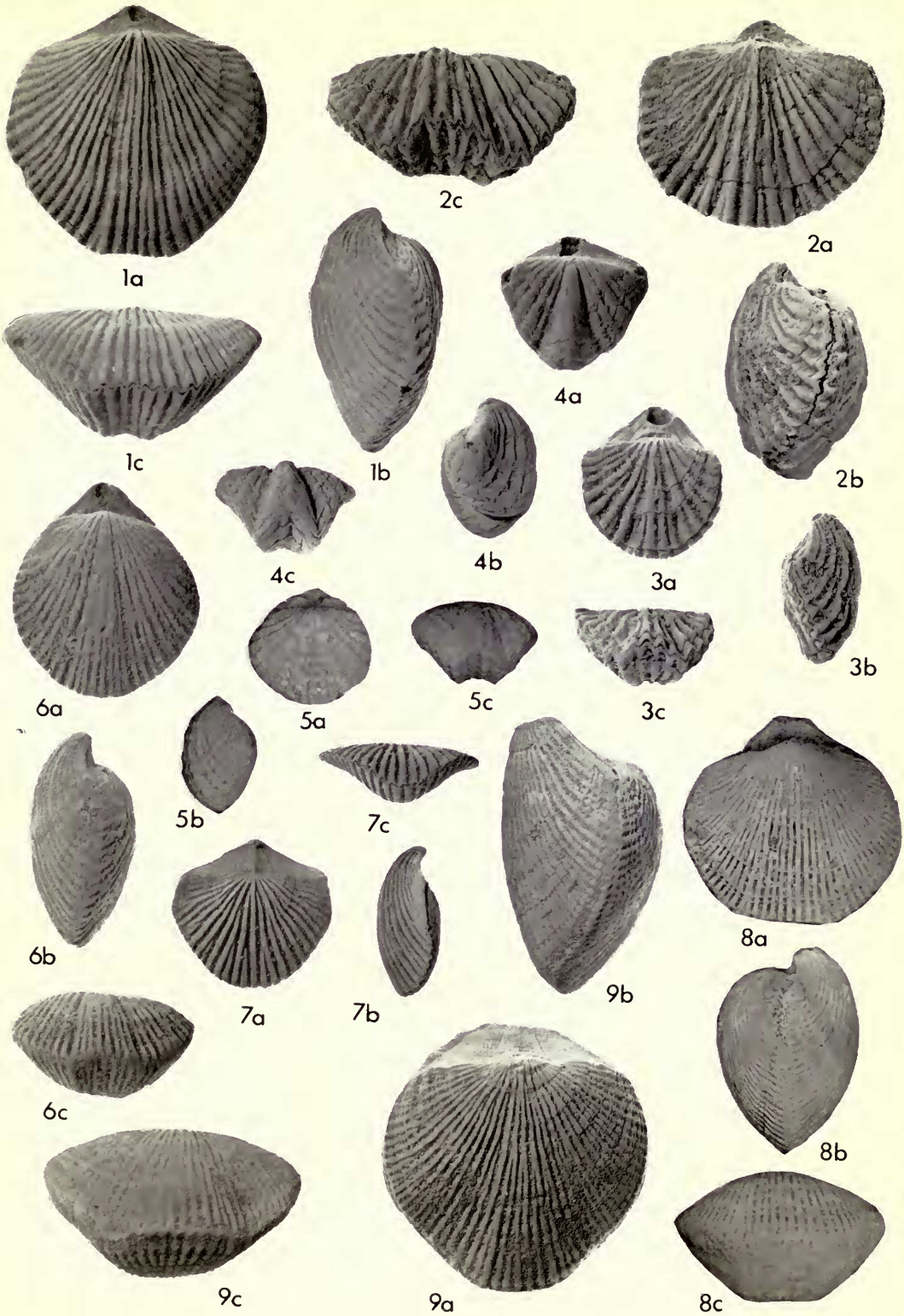
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PLATE 2

All specimens (except Figs 4) in Dept of Palaeontology,
British Museum (Natural History).
a. Dorsal view. b. Lateral view. c. Anterior view.

Gemmarcula pterygotos (Walker) (pp. 213, 221)

FIGS 1a, b, c. Lower Albian, *L. tardefurcata* Zone, Munday's Hill, Leighton Buzzard, Bedfordshire. BB 45967. × 2.

FIGS 2a, b, c. As above, showing numerous fine costae and thickened anterior margin. BB 45968. × 2.

Ismenia pectunculoides (Schlotheim) (p. 210)

FIGS 3a, b, c. Upper Jurassic, Nattheim, Württemberg, Germany. B 86059. × 2.

Terebratella kofoedi Ravn (p. 221)

FIGS 4a, b, c. Plaster cast. Middle Cenomanian, Madsegrav, Bornholm, Denmark. Original No. 1990 (Min. Geol. Mus. Univ. Copenhagen). × 2.

Helvetella arzierensis (de Loriol) (p. 222)

FIGS 5a, b, c. Valanginian, Arzier, Vaud, Switzerland. BB 61527. × 2.

Arenaciarcula acuticostata sp. nov. (p. 238)

FIGS 6a, b, c. Lower Albian, Munday's Hill, Leighton Buzzard, Bedfordshire. BB 45969. × 2.

Arenaciarcula beaumonti (d'Archiac) (p. 236)

FIGS 7a, b, c. Tourtia, Tournai, Belgium. BB 45970. × 2.

Arenaciarcula fittoni (Meyer) (p. 235)

FIGS 8a, b, c. Upper Aptian, Bargate Stone, Compton bypass, Surrey. B 95845. × 2.

Gemmarcula asteriana (d'Orbigny) (pp. 214, 224; see also Pl. 1, figs 6a–c)

FIGS 9a, b, c. Aptian, Sardiniero, Santander, Spain. BB 45971. × 2.

Oblongarcula oblonga (J. de C. Sowerby) (p. 230; see also Pl. 3, figs 1a–c)

FIGS 10a, b, c. Upper Aptian, Shanklin, Isle of Wight. BB 45972. × 2.

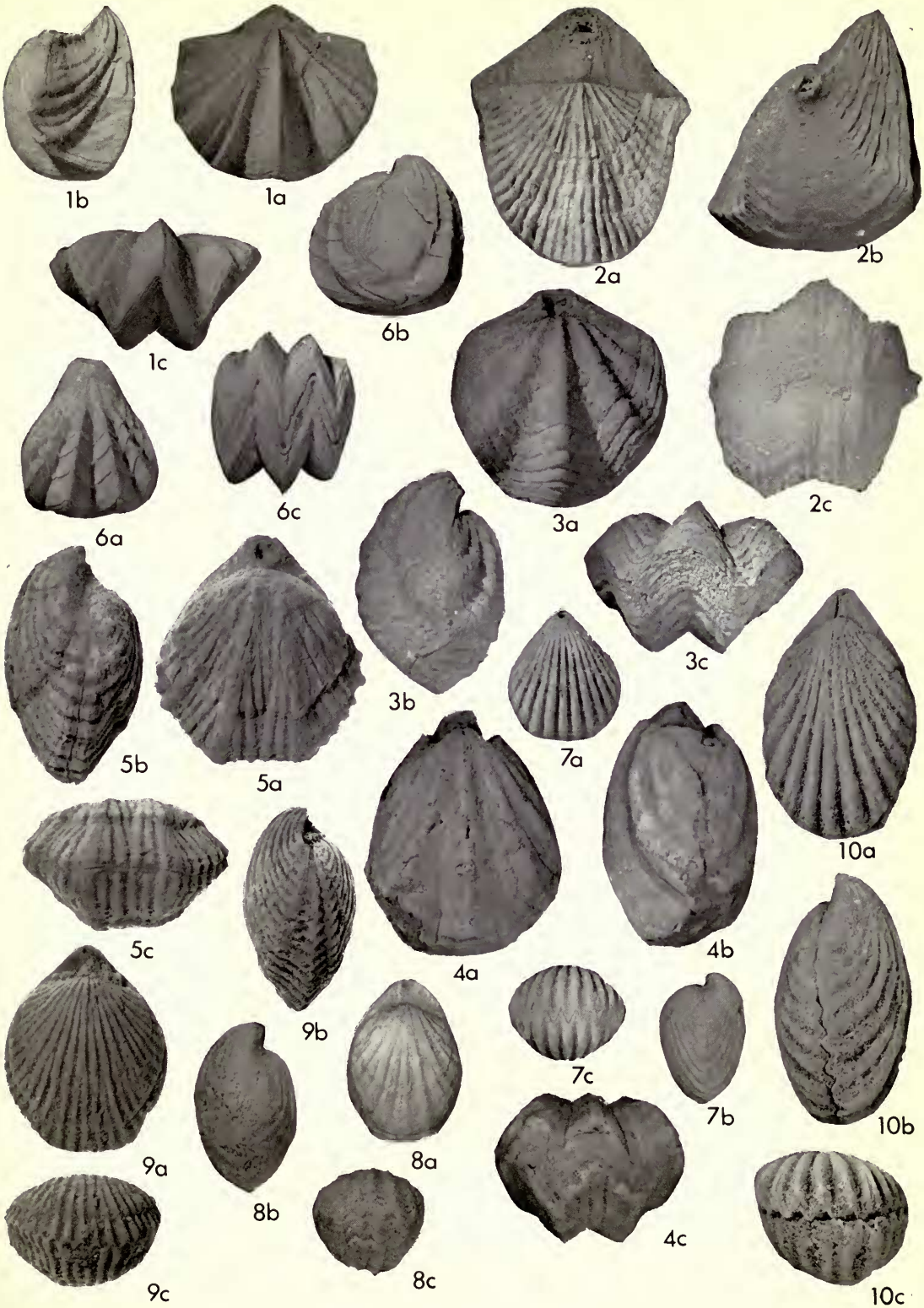
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PLATE 3

All specimens (except Figs 5–6) in Dept. of Palaeontology,
British Museum (Natural History)
a. Dorsal view. b. Lateral view. c. Anterior view.

Oblongarcula oblonga (J. de C. Sowerby) (p. 230 ; see also Pl. 2, figs 10a–c)

Figs 1a, b, c. Upper Aptian, Sponge Gravel, Faringdon, Berkshire. BB 45973. × 2.

Trigonosemus elegans Koenig (p. 241)

Figs 2a, b, c. Upper Chalk, Craie Phosphatée, Ciply, Belgium. BB 45974. × 2.

Arenaciarcula keepingi (Walker) (p. 240)

Figs 3a, b, c. Upper Aptian, Brickhill, Bletchley, Buckinghamshire. BB 45975. × 2.

Terebrirostra bargesana (d'Orbigny) (p. 249)

Figs 4a, b, c. Cenomanian, near La Bédoule, Bouches du Rhône, France. B 35187. × 1.

Oblongarcula alemannica sp. nov. (p. 227)

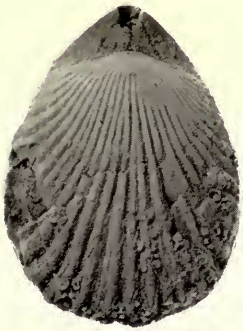
Figs 5a, b, c. Holotype. Hauterivian, Berklingen, north Germany. Roemer Mus. Hildesheim, No. RM 756. × 2.

Terebratella bornholmensis Ravn

Fig. 6. Plaster cast. Cenomanian, Madsegrav, Bornholm, Denmark. Original No. 1533 (Min. Geol. Mus. Univ. Copenhagen). × 2.

Oblongarcula davidsoni (Walker) (p. 233)

Figs 7a, b, c. Upper Aptian, Upware, Cambridge. BB 45976. × 2.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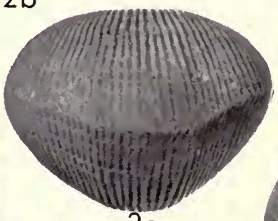
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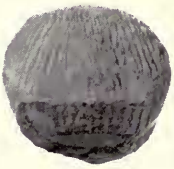
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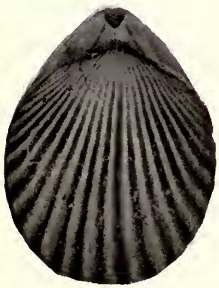
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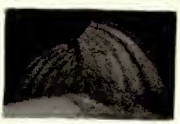
6


7c